Volume 21, Number 1

ISSN 1345-5834

June 2002

CURRENT HERPETOLOGY

FORMERLY *THE JAPANESE JOURNAL OF HERPETOLOGY*

Published by
THE HERPETOLOGICAL SOCIETY OF JAPAN
KYOTO

Current Herpetology.—Current Herpetology publishes original research articles on amphibians and reptiles. It is the official journal of the Herpetological Society of Japan and is a continuation of Acta Herpetologica Japonica (1964-1971) and Japanese Journal of Herpetology (1972-1999).

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Cover Illustration: A new depressed-bodied *Tropidophorus* from Vietnam. A photograph taken by Nikolai L. Orlov.

Current Herpetology 21(1): 1–8, June 2002

Foraging Behavior of *Rhabdophis tigrinus* (Serpentes: Colubridae) in a Gutter with a Dense Aggregation of Tadpoles

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Abstract: Field observations were made on the foraging behavior of *Rhabdophis tigrinus* in a gutter where numerous *Hyla japonica* larvae aggregated. It seemed that not only chemical cues but also visual cues play important roles in the foraging behavior in this snake. *Rhabdophis tigrinus* performed predatory behaviors characteristic of generalists, not of aquatic specialists. Examinations of stomach contents revealed that froglets were the dominant prey item although tadpoles were seemingly more abundant in the gutter. It is likely that this biased predation on froglets is attributable to the differential vulnerability to predation among the developmental stages of the frog. The present observations support the idea that *R. tigrinus* is not well adapted to an aquatic life. Possible significance of success ratio of predatory attempt as an index is discussed.

Key words: *Rhabdophis tigrinus*; Foraging behavior; Anuran larvae; Aquatic prey; Ratio of successful strike

INTRODUCTION

Snakes are all carnivorous predators that eat various types and sizes of prey, ranging from small invertebrates to large mammals (Mushinsky, 1987; Greene, 1997). From the viewpoint of feeding habits, each species is placed at a certain position on a continuum between two extremes, "generalist" and "specialist". The specialist often exhibits physiological, morphological, and/or behavioral adaptations to feed on a specific prey type (Gans, 1983; Mushinsky, 1987; Greene, 1997). To clarify the extent of the specialization in feeding habits in a particular species, field observation is desirable because natural surroundings influence animal behavior and place constraints on it that are often difficult to control in the laboratory.

Rhabdophis tigrinus is a medium-sized, diurnal colubrid snake commonly seen on the main islands (exclusive of Hokkaido) and adjacent islets of Japan (Stejneger, 1907). For this snake, there are a number of records in the literature that indicate its natural diet as consisting mostly of frogs, toads, and fish (Mori and Moriguchi, 1988). In regard to feeding behavior, Mori et al. (1992) reported a peculiar foraging behavior of *R. tigrinus* in the field, that is, a nocturnal

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ambush predation on the forest green tree frog, *Rhacophorus arboreus*. Under experimental conditions, Mori (1997) reported prey-handling behavior of the snake using frogs and fish as prey animals. However, although *Rhabdophis tigrinus* is generally considered semi-aquatic, little is known about how the snake forages for aquatic prey (e.g., fish, tadpoles) in the field and to what extent the snake is specialized for an aquatic life. In the present paper, I report foraging by *R. tigrinus* on aquatic and semi-aquatic prey observed in the field.

Materials and Methods

Field observations were made sporadically during the ecological survey of snakes on Yakushima Island (30°20′N, 130°32′E), Japan. Foraging behavior of *R. tigrinus* was observed in the gutter along the road named Seibu-rindo (Western Woodland Road). The road runs close to the western coast of the island and is surrounded by secondary forests. The gutter was 40 cm wide and contained up to 10 cm depth of still water, which I refer to as "the pool" (Fig. 1). Water of the pool was moderately clear (the bottom was clearly visible). The pool extended approximately 20 m along the gutter, and had the paved road on one side and a steep mountain slope on the other side. One end of the pool was overgrown with weeds, which I call "the weed area" (Fig. 1), and the opposite end was bare wet space covered with leaf litter and mud. At the center of the pool, leaf litter and mud formed another wet area, which I call "the land" (Fig. 1). Numerous *Hyla japonica* larvae of various developmental stages were observed in the pool.

In the initial three observations, I captured the snakes as soon as I saw them without observing their behavior. For these snakes, therefore, only the results of examination of the stomach contents are presented. In the other observations, behavior of the snakes was directly observed at distances of more than 2 m. These observations did not seem to disturb the subjects because no abrupt changes of behavior were evident. Each observation was terminated if the snake began to crawl out of the gutter or to enter the weed area. After most observations, the snakes were captured and their body temperatures were measured immediately to 0.1 C by inserting a thermistor bulb into the cloaca in the shade. Air and water temperatures were also measured. Stomach contents were forcibly ejected. Unless otherwise

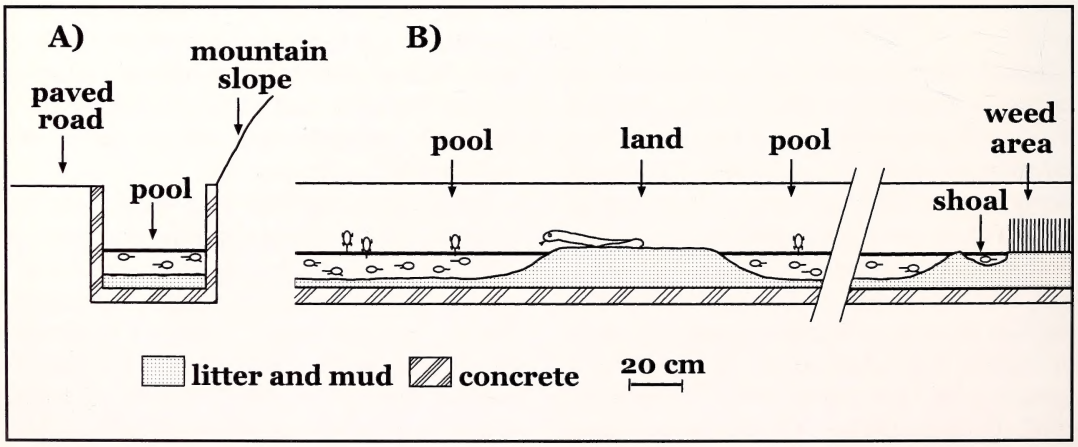

FIG. 1. Schematic diagrams of cross (A) and longitudinal sections (B) of the gutter. In the latter, a large part of the right pool is omitted (indicated by slanted lines) so as to depict all microenvironments in the gutter. Bold lines indicate the water surface level. Snake and anuran larvae are out of scale.

mentioned, recovered prey items were fixed in 10% formalin and preserved in 70% ethanol. At initial capture, each individual was brought to the field station, where it was measured for snout-vent length (SVL, measured to 1 mm by tape scale) and body mass (BM, up to 100 g, weighed to 0.1 g on an electric toploading balance; above 100 g, weighed to 1 g with a spring scale). The snake was then marked with paint on the head and by ventral scale clipping for individual recognition, and was released on the following day at the site of capture. Recaptured individuals were released immediately after body temperature measurement and examination of stomach contents.

RESULTS

A total of seven observations were made for three individuals (Table 1).

Observation 1: A snake, marked as no. 62, contained one tadpole of *H. japonica* and part of the forefoot of a *Bufo japonicus japonicus* in its stomach.

Observation 2: A snake, marked as no. 63, contained one tadpole and two froglets (defined here as Gosner's [1960] stages 43–45) of *H. japonica* in its stomach.

Observation 3: A snake, marked as no. 65, had no stomach contents.

Observation 4: No. 65 was found swimming in the pool. The snake reached the land, where it anchored its tail to dead twigs and started to peer into the pool. Suddenly, the snake lunged with the anterior part of the body (for convenience, I refer to this as a normal strike) into the water and swept its head from side to side several times with its mouth open. The snake seemingly responded to movements of a few tadpoles that were swimming near its head. Then the snake resumed peering, and after a few minutes it struck again, but this time it raised its head and neck immediately. After several minutes of wandering on the land, the snake exhibited another normal strike and succeeded in biting a tadpole at midbody (near developing hindlimbs), which it then swallowed tail first. Until capture, the snake continued prowling on the land or swimming in the pool with vigorous tongue flicking. The snake contained two tadpoles and nine froglets of *H. japonica* in its stomach. All strikes were made from the land, and success ratio of predatory attempts (SRPA: the number of successful strikes/the total number of strikes) was 0.33 (1/3).

Observation 5: No. 65 was found swimming in the pool. The snake crawled onto the dead leaves floating on the water surface and struck at a tadpole, but missed. Then the snake continued to swim with occasional tongue flicking. After several minutes, the snake crawled onto the land, and three normal strikes (two missed and one succeeded) at tadpoles followed the peering posture. Until disappearing into the weed area, the snake was swimming around in the pool or prowling on the land. SRPA was 0.25 (1/4).

Observation 6: No. 65 was found lying on the land with its body loosely coiled and peering into the pool. Suddenly, the snake moved its head slightly forward, probably in response to the movements of tadpoles. Then, the snake wandered about on the land or swam in the pool, and made two normal strikes at tadpoles from the land but neither of them succeeded. After a brief swim following these failures, the snake suddenly posed with its throat region contacting the wall of the gutter and with the remaining portion of the body floating in the pool. The anterior and posterior parts of the body formed an angle of 90°. From this posture, the snake protruded its head (I refer to this as floating strike), and captured a froglet clinging on the wall. After this success, three additional strikes were made at tadpoles that were either swimming in the pool or trapped in the shallow part. Of these strikes, two were made from the land and one from the pool with serpentine diving (mid-water diving with medium to fast locomotion and sinuous movements of head and body: Drummond, 1983). The strike was

TABLE 1. Data for *Rhabdophis tigrinus* taken at the time of capture in the gutter. Air temperature (T_a) was measured in shade at approximately 1 m above the ground. Water temperature (T_w) is expressed as that at the point of capture of a given snake (observation nos. 1–3), or as the range of temperatuers measured at different points in the pool (observation nos. 4–7). Body temperature (T_b) was measured in cloaca immediately after capture. The numbers of prey that were actually eaten in the gutter are given in parentheses. All tadpoles and froglets were identified as *Hyla japonica*.

Obs. no.	ID. no.	Sex	Date	Time	Weather	T_a (C)	T_w (C)	Tb (C)	SVL (mm)	BM (g)	Stomach contents
1	62	male	19 June 2001	08:52	fine	29.8	27.4	28.2	725	108	1 (0) tadpole; 1 (0) *Bufo j. japonicus*
2	63	male	20 June 2001	15:42	light rain	24.1	27.3	26.7	668	91.0	1 (0) tadpole; 2 (0) froglets
3	65	female	22 June 2001	14:23	fine	27.2	27.4	28.3	395	16.6	none
4	65	female	24 June 2001	13:35–13:55	fine	29.5	31.0–33.2	29.1	—	—	2 (1) tadpoles; 9 (0) froglets
5	65	female	25 June 2001	14:26–14:51	fine	32.6	30.2–35.6	—	—	—	not examined (1)**
6	65	female	28 June 2001	08:43–09:40	cloudy*	30.5	29.4–31.6	30.4	—	—	1 (1) tadpole; 2 (1) froglets
6	62	male	28 June 2001	09:28	cloudy*	30.5	29.4–31.6	30.7	—	—	none
7	65	female	29 June 2001	08:30–08:51	fine	27.0	28.0–29.4	28.5	—	—	15 (1) froglets

* It rained slightly during the observation.

** Stomach contents were not examined but predation on one tadpole was observed.

successful only for the trapped tadpole, which was swallowed head first. At this time, no. 62 was seen approaching no. 65. When the two snakes reached a point about 10 cm from each other on the land, no. 65 started to crawl rapidly, passed by the side of no. 62 and went away. I captured no. 62 at this time. No. 65 continued to swim in the pool and wander on the land, and the seventh normal strike (failure) was made from the land. No. 62 contained no prey in its stomach, whereas no. 65 contained one tadpole and two froglets of *H. japonica* in its stomach. These prey items were re-fed to the snake. SRPA for no. 65 was 0.29 (2/7).

Observation 7: No. 65 was found swimming in the pool. The snake made a floating strike at a froglet clinging on the wall, but the prey escaped. Then, it briefly repeated the pose with its snout touching the wall of the gutter several times while swimming until it made a successful normal strike at a froglet in the shoal. After this success, the snake repeated the snout touching behavior described above, and made a floating strike (failure) at a froglet clinging on the wall. The snake contained 15 froglets of *H. japonica* in its stomach. I judged that the prey items were all newly ingested (i.e., not including the two froglets that were re-fed on the previous day: see above) by the degree of digestion. All prey were re-fed to the snake. SRPA was 0.33 (1/3). Total SRPA of no. 65 throughout the observation period was 0.29 (5/17).

Discussion

The importance of chemical cues in the snake feeding behavior has been demonstrated by numerous experimental studies (see Burghardt [1990]; Halpern [1992] for review). Snakes transfer chemicals to chemoreceptive organs that are situated on the roof of the oral cavity by either tongue flicking or snout touching (Halpern and Kubie, 1980). It is, therefore, likely that the tongue flicking and snout touching behavior observed in the present study indicates that the snakes were searching for prey using chemical cues. On the other hand, both laboratory experiments and field observations indicate that visual cues also play an important role in the feeding behavior of snakes (e.g., Czaplicki and Porter, 1974; Herzog and Burghardt 1974; Drummond, 1985; Ota, 1986; Heinen, 1995). The present observations suggest that in the predatory behavior of *R. tigrinus*, visual cues, especially those from prey movements, are also important, because on several occasions normal strikes occurred immediately after movements of the tadpoles.

Hyla japonica larvae of various developmental stages formed dense schools in the pool. Froglets were the dominant prey recovered from the snakes' stomachs, although tadpoles were seemingly more abundant (about 10 times or more) than froglets in the pool. Both laboratory and field studies have indicated that anurans are particularly vulnerable to snake predation during the metamorphic transition (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). This vulnerability during the metamorphic transition is attributed to the locomotor ineptitude of transforming anurans: froglets can neither swim nor hop as effectively as tadpoles or frogs, respectively (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). In this study, predatory events actually observed were only against three tadpoles and two froglets. Therefore, it may be possible that the prey recovered from the snakes' stomachs were taken at some other place where froglets were more abundant than in the gutter. Such a situation, however, is actually unlikely because (1) the area surrounding the gutter was relatively dry and lacked possible habitats for tadpoles and metamorphosing froglets, such as swamps and streams; (2) in froglets recovered from the snakes' stomachs, the tail was not yet fully absorbed, making it unlikely that they had already dispersed far away from the tadpoles' habitat when eaten by the snakes; and (3) the degree of digestion was almost

identical in all prey exclusive of *B. japonicus*, indicating that all predatory events involving *H. japonica* tadpoles and froglets had occurred in a fairly short period. Thus, I believe that all *H. japonica* tadpoles and froglets recovered from the snakes' stomachs were taken in the gutter, and that the biased predation toward froglets (five tadpoles vs. 28 froglets) was the consequence of a greater vulnerability to predation in froglets than in tadpoles in *H. japonica*.

Drummond (1983) described aquatic foraging in garter snakes and a water snake. In his study, "generalists" exhibited characteristic behaviors such as open-mouth searching and serpentine diving in mid-water, whereas "aquatic specialists" exhibited other characteristic behaviors such as substrate-crawling and mid-water pursuit (rapid locomotion toward prey in mid-water). *Rhabdophis tigrinus* in the present observations performed open-mouth searching and serpentine diving, but substrate-crawling and mid-water pursuit were never observed. Under experimental conditions, *R. tigrinus* was inefficient in capturing fish, and fish once grasped by the snake frequently escaped during handling (Mori, 1997). Furthermore, the snake always handled and swallowed fish on land (Mori, 1997). Mori (1997) assumed that these behavioral propensities reflect incomplete adaptation of this snake to an aquatic life. The present observations seem to support this postulation, although further field observations on more individuals are definitely needed to draw firm conclusions on this problem.

Several studies reported foraging behavior and its efficiency in actively foraging snakes including both dietary generalists and specialists in the field. Wendelken (1978) observed that *Thamnophis proximus* (a putative specialist on amphibian prey: Rossman et al., 1996) chased 10 frogs but none were captured during 45 min. Patterson and Davies (1982) reported that in spite of a high abundance of fish in a river, only one out of many individuals of *Natrix maura* (a putative specialist on fish prey: Hailey and Davies, 1986; Santos and Llorente, 1998) there caught a fish in several hours' observation. Hailey and Davies (1986) reported that 48 individuals of *N. maura* made 124 strikes at fish throughout a total of 921 min observation, and only two made contact. Ota (1986) reported that SRPA against lizards by *Elaphe quadrivirgata* (a putative dietary generalist: Mori and Moriguchi, 1988) was 0.125 (2/16). Balent and Andreadis (1998) reported that *Nerodia sipedon* (a putative aquatic and dietary specialist on fish prey: Drummond, 1983) did not succeed in capturing aquatic prey in any of 17 attempts throughout a total of 44.75 min observation. In the present observations, total SRPA of *R. tigrinus* (no. 65) was slightly higher (0.29) than in these previous studies. However, three out of the five successful strikes involved either a tadpole trapped in a shoal or froglets, and these prey would have been captured more easily than tadpoles in free water because of their locomotory impediment. Therefore, it seems that SRPA of *R. tigrinus* against aquatic prey is not so high as expressed by the above figures.

Can we, however, infer the extent of specialization of the subject species only on the basis of SRPA as an indicator? In the studies cited above, foraging success is not higher in the specialists than in the generalists. This suggests that low SRPA does not always indicate less adaptation to a particular type of microhabitat (e.g., aquatic, terrestrial, arboreal) or of prey, because various external (e.g., temperature, light condition, prey density) and internal factors (e.g., age and body condition of either prey or predator) would affect foraging efficiency. For better understanding of the biological and evolutionary significance of SRPA, further field observations on both active foragers and ambushers are desirable.

ACKNOWLEDGMENTS

I am grateful to A. Mori for valuable

comments on the manuscript and T. Hirai for helping with identifications of items regurgitated by snakes. I also thank two anonymous reviewers for helpful comments on an early version of the manuscript, and S. Horiuchi, H. Kudo, T. Teramura, and R. Tsujino for their hospitality during my stay at the Kyoto University Yakushima Field Station during the fieldwork.

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Accepted: 11 April 2002

Current Herpetology 21(1): 9–23, June 2002

Three New Depressed-bodied Water Skinks of the Genus *Tropidophorus* (Lacertilia: Scincidae) from Thailand and Vietnam

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Abstract: Three new species of the genus *Tropidophorus*, characterized by distinct depression of body, strongly keeled lateral body scales, and saxicolous habits, are described from Indochina. Of these, two moderately depressed species, one with undivided frontonasal and widened paravertebral scales, and the other with divided frontonasal and unwidened paravertebral scales, were collected from small areas in northeastern and eastern Thailand, respectively. The remaining species with extremely depressed head and body was found from one limited area in northern Vietnam. The three species most resemble *T. baviensis* Bourret, 1939 from northern Vietnam among the known congeneric species in body size, body shape, and scutellation. However, body depression in *T. baviensis* is not so prominent as in the present three species. Considering that most specimens of these species were collected from rock crevices, their characteristic body shapes may represent certain stages of adaptation to life in crevices.

Key words: *Tropidophorus*, Scincidae, Thailand, Vietnam, New species, Taxonomy, Body depression, Rock crevices

INTRODUCTION

Tropidophorus is a group of approximately 20 species of small to moderate sized lygosomine skinks distributed in Bangladesh, southern China, and Southeast Asia including the Philippines (Welch et al., 1990; Wen, 1992). This genus is characterized by superficial location of the tympanum, and most of its species are known to prefer semiaquatic

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habitats along forest streams (e.g., Taylor, 1963; Brown and Alcala, 1980).

During recent herpetological surveys in Indochina, specimens of skinks, characterized by distinctly depressed bodies with strongly keeled lateral scales, were collected from three localities, two in Thailand and one in Vietnam (Fig. 1). These skinks possessed superficial tympanums and thus were identified as members of the genus *Tropidophorus*. They most resembled *T. baviensis* Bourret, 1939 from northern Vietnam in body size, body shape, and scutellation, but differed from the latter or any other congeneric species so far described by distinct depression of body. Also, specimens from the three localities showed substantial differences from each other in a number of morphological characters. We thus describe three new species of *Tropidophorus* on the basis of these specimens.

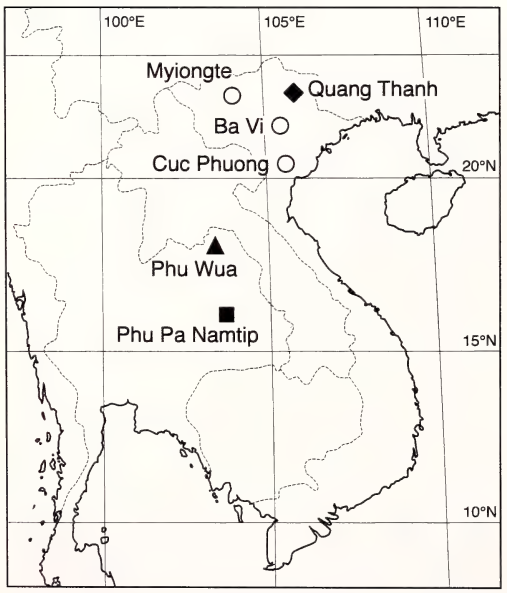

FIG. 1. Known localities of the three depressed-bodied *Tropidophorus* and *T. baviensis*. Open circles, *T. baviensis*; closed rectangle, *T. matsuii* sp. nov.; closed triangle, *T. latiscutatus* sp. nov.; and closed diamond, *T. murphyi* sp. nov.

MATERIALS AND METHODS

The specimens, euthanized with diethyl ether or nembutal solution, were fixed with 10% buffered formalin, soaked in water, and preserved in 75% ethanol. Then measurements were taken to the nearest 0.1 mm with dial calipers. Initially all specimens were numbered according to the reference systems of the Zoological Collection, Kyoto University Museum (KUZ), and the Field Number, Royal Ontario Museum (Field No. ROM). Some of them were then moved to the Zoological Collections of Thailand Natural History Museum (TNHM), Royal Ontario Museum (ROM), Zoological Institute, Russian Academy of Sciences, St Petersburg (ZISP), and Natural History Museum of Chulalongkorn University (CUMZ).

Five specimens of *T. baviensis*, deposited in Muséum National d'Histoire Naturelle, Paris (MNHN: holotype) and ZISP were used for comparisons (see Appendix). Comparisons with the other congeneric species were made on the basis of literature descriptions (Smith, 1923, 1935; Taylor, 1963; Brown and Alcala, 1980; Wen, 1992).

Ngo et al. (2000), in a recent redescription of *T. baviensis*, followed Peters' (1964) "Dictionary of Herpetology" in the use of terms to refer to each scale character. However, the terminology of Peters (1964) is not actually the standard for scincid squamation, and thus is not suitable for comparisons using descriptions in previous publications (Smith [1923, 1935], Taylor [1963], etc.). Therefore, we chiefly followed Taylor's (1936) terminology, which has enjoyed a far more common use in publications dealing with scincid taxonomy. The paravertebral scales were defined following Greer (1982) as middorsal scales from the posterior end of the parietals to the posterior margin of the thigh. The postsupraocular was defined as referring to a small scale posterior to the supraocular series. Of the measurements, head length was defined as the distance from the tip of the snout to the posterior margin of one of

the parietals or the interparietal (whichever was more distant). Snout length was measured from the tip of the snout to the anterior margin of the eye. Presacral vertebrae were counted by use of autoradiography (Softex, Softex Co.).

Tropidophorus latiscutatus sp. nov.
(Figs. 2 and 3)

Holotype

Adult male, TNHM-R-60001 (KUZ R40362), from Phu Wua Wildlife Sanctuary (18°05′N, 103°45′E, altitude ca 200 m), Nong Kai Province, eastern Thailand, collected by M. Matsui, H. Ota, M. Toda, K. Araya, and J. Nabhitabhata on 21 October 1996.

Paratypes

Five males, TNHM-R-60002 (KUZ R40258), TNHM-R-60003 (KUZ R40370), KUZ R40256, KUZ R40377 and ZISP 22264 (KUZ R40407), and four females, TNHM-R-60004 (KUZ R40373), TNHM-R-60005 (KUZ R40257), KUZ R40259 and CUMZ R 2002.295 (KUZ R45908), from the same locality as the holo-

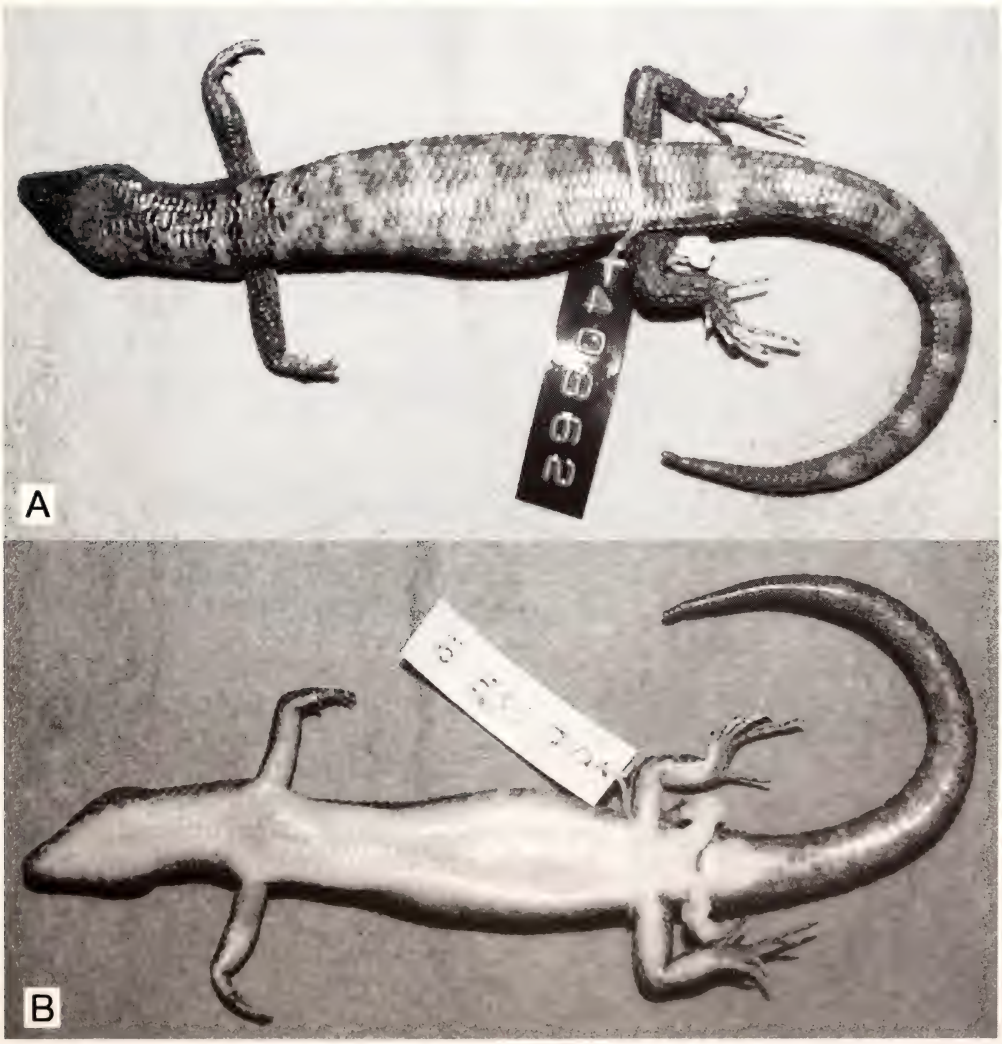

FIG. 2. Dorsal (A) and ventral (B) views of *Tropidophorus latiscutatus* sp. nov. (holotype, TNHM-R-60001).

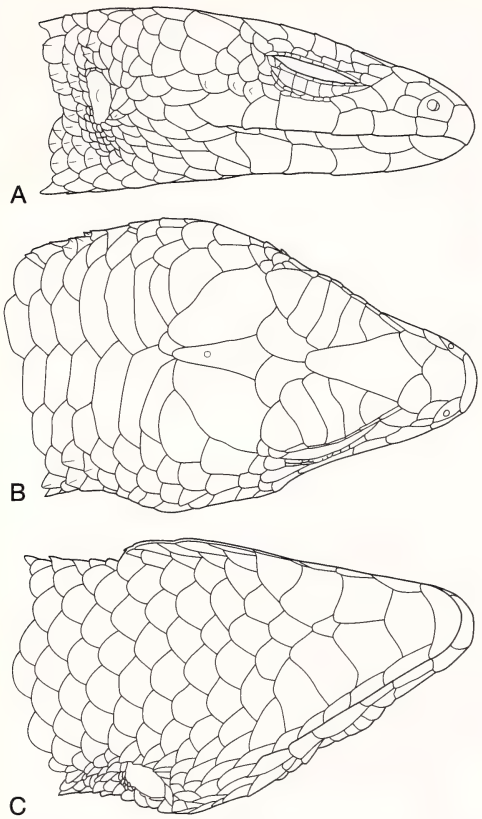

FIG. 3. Lateral (A), dorsal (B), and ventral (C) views of head scales of *Tropidophorus latiscutatus* sp. nov. (holotype, TNHM-R-60001).

type, collected from 20 to 23 October 1996.

Diagnosis

A *Tropidophorus* with moderately depressed head, body, and tail; scales on dorsal surface of head smooth as a whole, but those in temporal region more or less keeled; frontonasal undivided; 6–7 superciliaries; paravertebral scales smooth or feebly keeled, twice as broad as neighboring scales; 58–63 paravertebral scales; dorsolateral and lateral scales distinctly keeled; usually 28 (but rarely 30) midbody scale rows. See Discussion for comparisons with other congeneric species.

Description of holotype

Snout rounded, rostral partly visible from above; no supranasals; frontonasal undivided, overlapped by rostral, nasals, and upper anterior loreals, and overlapping prefrontals and frontal; prefrontals separated, overlapped by frontonasal, upper anterior, and posterior loreals, and overlapping frontal, first supraoculars, and first superciliaries; frontal large, narrowing posteriorly, overlapped by frontonasal and prefrontals, and overlapping first, second, and third supraoculars and frontoparietals; supraoculars four, first one divided into upper and lower elements, overlapped by superciliaries; seven superciliaries; interparietal smaller than frontal, narrowing and slightly concave posteriorly, overlapping parietals; small transparent spot on interparietal, showing location of parietal foramen; parietals separated by interparietal; nuchals four on left, three on right, anteriormost ones separated; nostril piercing nasal; nasal overlapped by rostral and first supralabial, and overlapping frontonasal and two anterior loreals; both anterior loreals overlapped by nasal, and overlapping posterior loreal; lower anterior loreal overlapping upper one, and very slightly overlapped by second supralabial, contacting first supralabial at point; supralabials six, three anterior to, one just beneath, and two posterior to orbit; shallow groove running on loreal-labial border, posteriorly crossing subocular in obliquely downward direction; two presuboculars, anterior one larger than posterior one, overlapped by posterior loreal and supralabials; lower eyelid with seven scales, separated from labials by two or three rows of granular scales; postocular single, overlapped by fourth supraocular and palpebrals, overlapping postsuboculars; postsupraocular overlapped by fourth supraocular and postocular, and overlapping parietal and primary temporal; postsuboculars four, first one overlapped by fourth supralabial, and overlapping fifth supralabial; temporals in seven rows, those in secondary and tertiary rows more or less enlarged, the uppermost row largest, and overlapped by parietal; temporals in the other rows as large as body scales; tympanum superficial; mental overlapping first

infralabials and postmental; postmental undivided, overlapped by mental and first infralabials, and overlapping first pair of chinshields; chinshields in three pairs, first left one overlapped by first right one, second pair separated by single scale, and third pair separated by three scales; five infralabials; 28 midbody scale rows; 13 scale rows at position of tenth subcaudal on tail; paravertebral scales 59, twice as broad as neighboring scales, smooth or feebly keeled on body and base of tail, and distinctly keeled on the remaining portion of tail; scales in row adjacent to paravertebral row on each side, weakly keeled on neck, body and tail; dorsolateral and lateral scales distinctly keeled; eight rows of midventral scales smooth, scales in outer row on each side feebly keeled; preanals two, enlarged, right overlapped by left; subcaudals smooth, first one four times as broad as neighboring scales, remaining ones only two times as broad as neighboring keeled scales; scales on forelimbs keeled, those on hindlimbs keeled dorsally, but smooth ventrally; 18–20 subdigitals on fourth toe. Presacral vertebrae 26.

Testes enlarged, 9.2 mm in longer axis; epdidymides regressed.

Measurements of holotype (mm)

Snout-vent length (SVL), 91.3; tail length, 96.0 (21.0 in regenerated portion); snout to forelimb length, 33.5; head length, 16.4; head width, 13.7; head depth, 8.1; snout length, 6.2; eye length, 5.2; eye to tympanum length, 7.7; snout to tympanum length, 18.0; tympanum height, 3.3; tympanum width, 2.7; axilla to groin length, 48.3; midbody width, 18.0; midbody depth, 8.5; forelimb length, 24.3; hindlimb length, 32.4; fourth toe length, 11.2.

Color in preservative

Dark brown on dorsal and lateral surfaces of head, body, and tail; two, nine, and ten transverse bands, pale brown in color and rather irregular in shape, on dorsal surfaces of neck, body, and tail, respectively; several pale brown spots on supralabials and infralabials; yellowish ivory on gular, and ventral surfaces of body and proximal portion of tail; distal portion of tail brownish yellow ventrally.

Color in life

Dorsal and lateral surfaces somewhat darker than after preservation (see above).

Variation

Of paratypes, four adult males and two adult females measured 82.1–94.3 and 93.8–102.0 mm in SVL, respectively, whereas SVLs in three immature females ranged from 60.2 to 66.4 mm. The number of paravertebrals varied from 59 to 63 in males and from 58 to 62 in females. The number of midbody scale rows was 28 in eight paratypes, but 30 in the one remaining paratype. Upper and lower anterior loreals were fused on one side in two specimens, and on both sides in one specimen. Nuchals were in two or three pairs in paratypes. Supralabials were invariably six. Infralabials were usually five, but rarely six or four. Superciliaries were usually seven, but rarely six. In paratypes, first supraocular was not divided as in holotype. Frontal contacted usually two, but rarely three supraoculars. The number of subdigitals ranged from 18 to 22. The number of scale rows on tail at position of tenth subcaudal was usually 13, but rarely 14 or 15. In two male paratypes, portions pale brown in preservative were somewhat reddish in life. Such a reddish tint was not recognized in the other individuals in life.

Etymology

The name is derived from the Latin words, *latus* (broad) and *scutum* (scale), referring to the distinctly widened paravertebral scales characteristic of this species.

Natural history

Most specimens, including the holotype, were found in the daytime in crevices of a few large rocks and outcrops on the weak

slope of a flattened sandstone hill. Though surrounded by relatively dry open forest, the substrates beneath these rocks and outcrops were marshy, and the insides of the crevices at their lower portions (<20 cm), from which the skinks were collected, were highly moist and partially wet. Crevices at higher portions were less moist and occasionally occupied by other lizards, such as *Mantheyus phuwuanensis* and *Cyrtodactylus* spp. In the evening (after sunset), two *T. latiscutatus* were found active on the ground near one of those rocks, and this suggests that this species is nocturnal.

Tropidophorus matsuii sp. nov.
Figs. 4 and 5

Holotype

Adult male, TNHM-R-60006 (KUZ R40540), from Phu Pa Namtip (15°53′N, 104°18′E, altitude 350 m), Roi Et Province, eastern Thailand, collected by M. Toda and K. Araya on 25 October 1996.

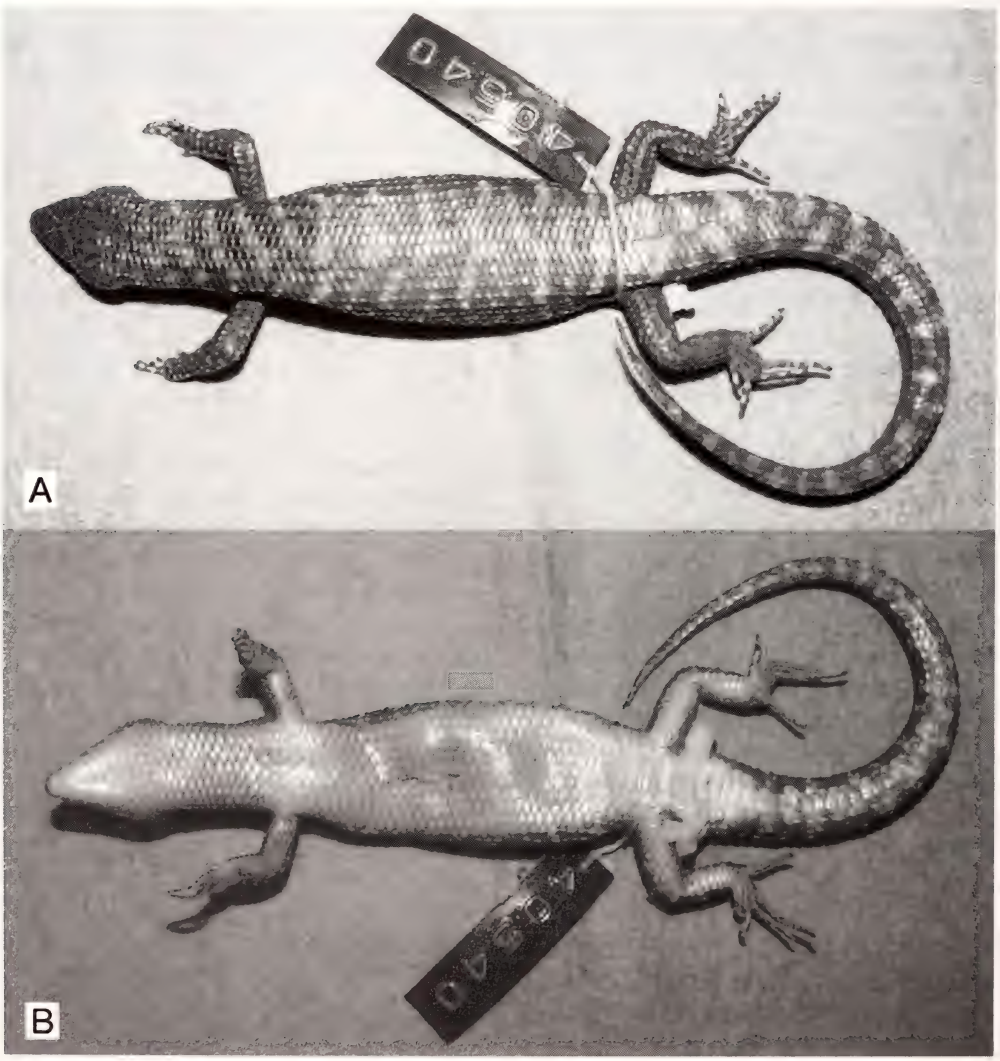

FIG. 4. Dorsal (A) and ventral (B) views of *Tropidophorus matsuii* sp. nov. (holotype, TNHM-R-60006).

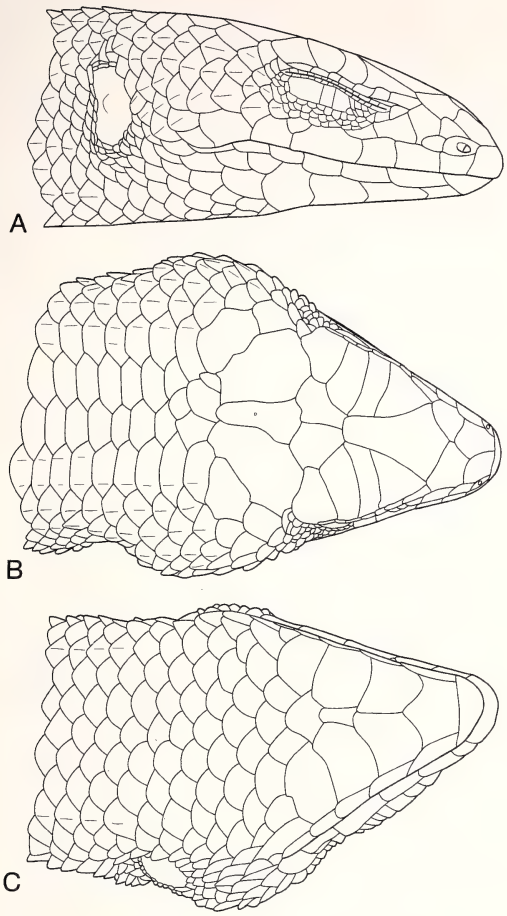

FIG. 5. Lateral (A), dorsal (B), and ventral (C) views of head scales of *Tropidophorus matsuii* sp. nov. (holotype, TNHM-R-60006).

Paratypes and other specimens

None.

Diagnosis

A *Tropidophorus* with moderately depressed head, body, and tail; scales on dorsal surface of head smooth as a whole, but those in temporal region keeled; frontonasal divided; eight superciliaries; paravertebral scales smooth or feebly keeled, subequal to neighboring scales in size; 65 paravertebral scales; dorsolateral and lateral scales distinctly keeled; 34 midbody scale rows. See Discussion for comparisons with other congeneric species.

Description of holotype

Snout rounded, rostral partly visible from above; no supranasals; frontonasal divided with right element smaller than left one, overlapped by rostral, nasals, and upper anterior loreals, and overlapping prefrontals; prefrontals overlapped by frontonasals, upper anterior, and posterior loreals, and overlapping frontal, first supraoculars, and first superciliaries; right prefrontal narrowly overlapped by left one; frontal large, narrowing posteriorly, overlapped by prefrontals, and overlapping first and second supraoculars and frontoparietals; supraoculars four, overlapped by superciliaries; eight superciliaries; interparietal smaller than frontal, narrowing and slightly concave posteriorly, and overlapping parietals; small transparent spot on interparietal, showing location of parietal foramen; parietals separated by interparietal; nuchals lacking; nostril piercing nasal; nasal overlapped by rostral and first supralabial, and overlapping frontonasal and two anterior loreals; both anterior loreals overlapped by nasal, and overlapping posterior loreal; lower anterior loreal overlapping upper anterior loreal and very slightly second supralabial, and contacting first supralabial at point; upper anterior loreal overlapping frontonasal and prefrontal; supralabials six, three anterior to, one just beneath, and two posterior to orbit; shallow groove running on loreal-labial border, posteriorly crossing subocular in obliquely downward direction; two presuboculars, anterior one larger than posterior one, overlapped by posterior loreal and supralabials; lower eyelid with six scales, posterior three extremely enlarged, separated from labials by three rows of granular scales; three small postoculars, overlapped by fourth supraocular and palpebrals, and overlapping postsuboculars; postsupraocular overlapped by fourth supraocular and postoculars, and overlapping parietal, primary temporal, and postsuboculars; postsuboculars five, first one smooth, overlapped by fourth supralabial and overlapping fifth supralabial, remaining four postsuboculars keeled; temporals in seven

rows, those in secondary and tertiary rows more or less enlarged, uppermost rows largest, smooth, overlapped by parietal, the others smaller, keeled; temporals in the other rows keeled, subequal to body scales in size, upper ones directed straight backward, lower ones directed obliquely downward; tympanum superficial; mental overlapping first infralabials and postmental; postmental undivided, overlapped by mental and first infralabials, and overlapping first chinshields; chinshields in three pairs, first right one overlapping first left one, second pair separated by single scale, third pair separated by three scales; six infralabials; one postgenial following each of third chinshields; 34 midbody scale rows; 15 scale rows at position of tenth subcaudal on tail; paravertebrals 65, subequal in size to neighboring scales, with two very weak keels on neck, smooth on body and base of tail, and with one moderate keel on the remaining portion of tail; scales in row adjacent to paravertebral row on each side with two weak keels on neck, and with single weak keel on body and tail; dorsolateral and lateral scales distinctly keeled; eight rows of mid-ventral scales smooth, scales in outer row on each side feebly keeled; preanals two, enlarged, right one overlapped by left one; subcaudals smooth anteriorly, weakly keeled posteriorly, first one four times as broad as neighboring scales, remaining ones only two times as broad as neighboring keeled scales; scales on ventral surfaces of hindlimbs only feebly keeled, those on the other portions of hindlimbs and on forelimbs distinctly keeled; 22–23 subdigitals on fourth toe. Presacral vertebrae 26.

Testes regressed, 6.6 mm in longer axis; epididymides regressed.

Measurements of holotype (mm)

SVL, 94.1; tail length, 113.0; snout to forelimb length, 34.2; head length, 15.9; head width, 14.7; head depth, 8.9; snout length, 6.1; eye length, 5.5; eye to tympanum length, 7.6; snout to tympanum length, 18.0; tympanum height, 3.6; tympanum width, 2.2; axila to groin length, 50.2; midbody width, 20.1; midbody depth, 9.6; forelimb length, 26.1; hindlimb length, 35.7; fourth toe length, 11.0.

Color in preservative

Dark brown on dorsal and lateral surfaces of head, body, and tail; three, nine, and 23 transverse bands, pale brown in color and somewhat irregular in shape, on dorsal surfaces of neck, body, and tail, respectively; several irregular pale brown spots on lateral sides of body (Fig. 2); several pale brown spots on supralabials and infralabials; yellowish ivory on gular and venter; ventral surface of tail yellowish ivory with indistinct dark flecks.

Color in life.

Dorsal and lateral surfaces slightly darker than after preservation; portions light brown in preservative (see above) with somewhat orange tint.

Etymology

The name is dedicated to Prof. Masafumi Matsui of Kyoto University, the project leader of the herpetological survey in Thailand, during which the present species was discovered.

Natural history

The single type specimen was found in a crevice of the lower portion of a sandstone outcrop, surrounded by relatively humid evergreen forest. Two gekkonid lizards, *Cyrtodactylus papollionoides* and *Gekko petricolus*, were also found in crevices of sandstone rocks near the collecting site.

Tropidophorus murphyi sp. nov.
(Figs. 6–8)

Holotype

Adult male, ROM 41227 (ROM field No. 27044), from Quang Thanh Village (22°37′43 N, 105°54′46 E, altitude 700–750 m), Nguyen Binh District, Cao Bang

Province, northern Vietnam, collected by R. W. Murphy, N. L. Orlov, A. Lathrop, T. Mason, S. Riabov, and T. C. Ho in May 1998.

Paratypes

Four males, ROM 41220 (ROM Field No. 26739), 41222 (Field No. 26960), 41223 (Field No. 26961) and 41226 (Field No. 27002), and seven females, ROM 41221 (ROM Field No. 26959), 41224 (Field No. 27000), 41225 (Field No. 27001), 41228 (Field No. 27045), 41229 (Field No. 27058), 41230 (Field No. 27059) and KUZ R58270 (Field No. 27003), with same sampling data as the holotype.

Diagnosis

A *Tropidophorus* with extremely depressed head, body, and tail; head scales smooth on dorsal surface, but rugose on lateral surfaces; frontonasal undivided; 6–8 superciliaries;

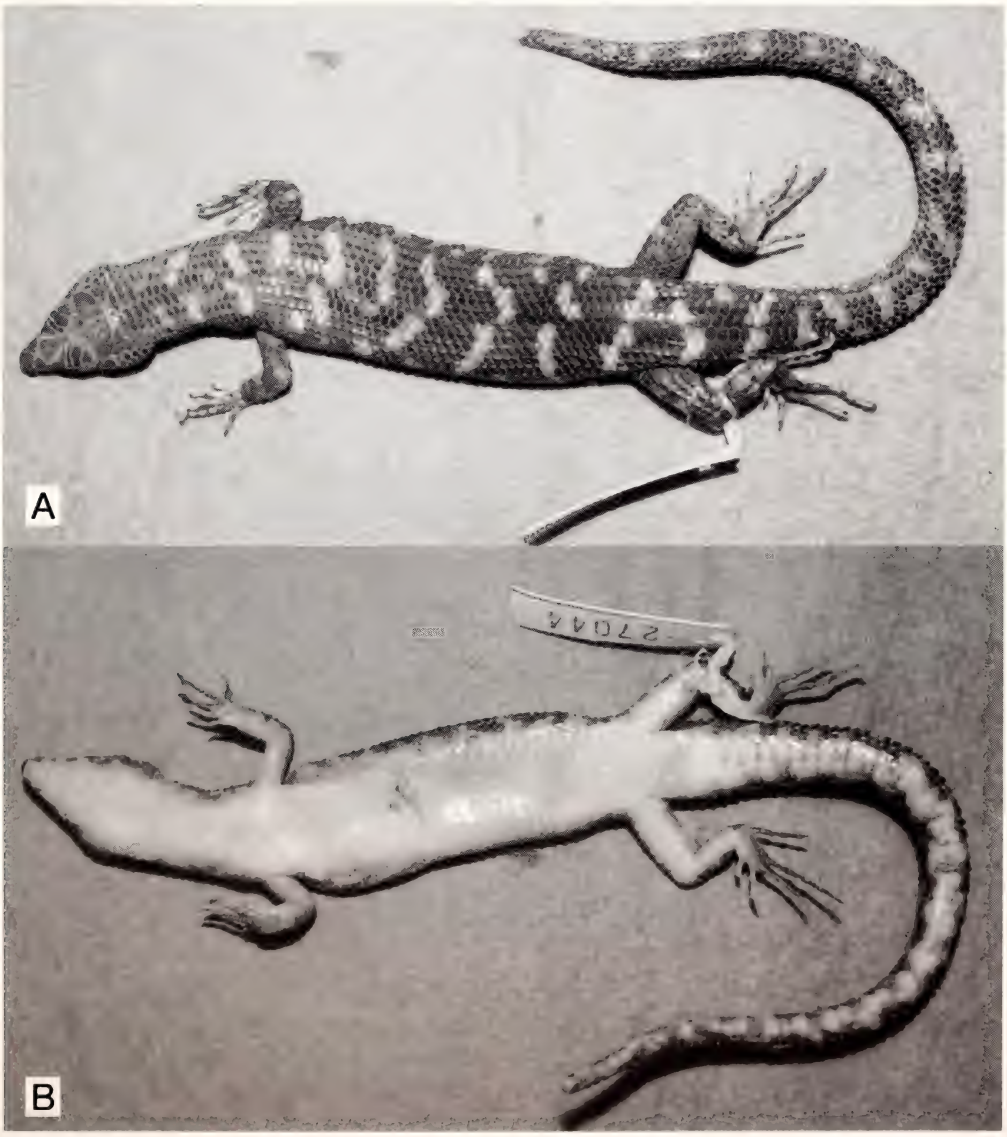

FIG. 6. Dorsal (A) and ventral (B) views of *Tropidophorus murphyi* sp. nov. (holotype, ROM 41227).

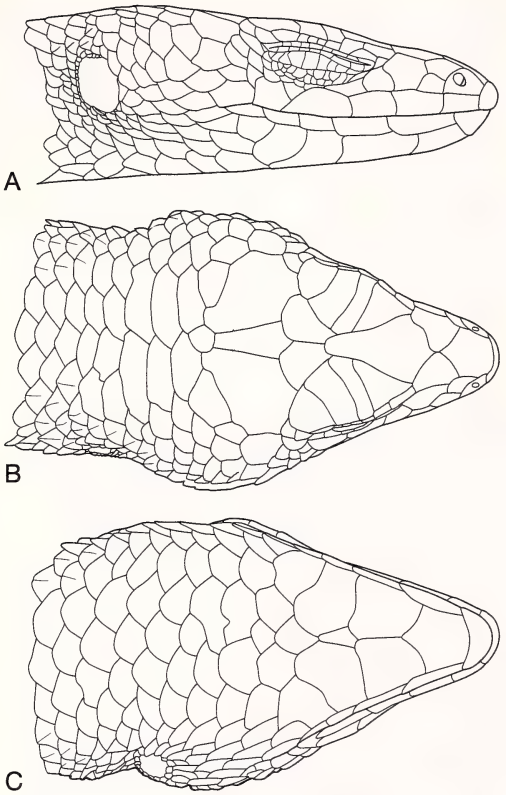

FIG. 7. Lateral (A), dorsal (B), and ventral (C) views of head scales of *Tropidophorus murphyi* sp. nov. (holotype, ROM 41227).

paravertebral scales smooth or feebly keeled, subequal to neighboring scales in size; 55–67 paravertebral scales; dorsolateral and lateral scales distinctly keeled; 30–32 midbody scale rows. See Discussion for comparisons with other congeneric species.

Description of holotype

Snout rounded, rostral partly visible from above; no supranasals; frontonasal undivided, overlapped by rostral, nasals, and upper anterior loreals overlapping prefrontals; prefrontals contacting each other at point, overlapped by frontonasals, upper anterior and posterior loreals, and overlapping frontal, first supraoculars, and first superciliaries; frontal large, narrowing postriorly, overlapped by prefrontals, and overlapping first and second supraoculars and frontoparietals; supraoculars four, overlapped by superciliaries; superciliaries six in left, seven in right; interparietal smaller than frontal, narrowing and slightly concave posteriorly, overlapping parietals; small transparent spot on interparietal, showing location of parietal foramen; parietals separated by interparietal; three pairs of nuchals; nostril piercing nasal; nasal overlapped by rostral and first supralabial, and overlapping frontonasal and two anterior loreals; both anterior loreals overlapped by nasal, and overlapping posterior loreal; lower anterior loreal very slightly overlapped by second supralabial, and overlapping upper anterior loreal, but not contacting first supralabial; upper anterior loreal overlapping frontonasal and prefrontal; supralabials six, three anterior to, one just beneath, and two posterior to orbit; shallow groove running on loreal-labial border, posteriorly crossing subocular in obliquely downward direction; two presuboculars, anterior one larger than posterior one, overlapped by posterior loreal and supralabials; lower eyelid with seven scales, separated from labials by two or three rows of granular scales; two postoculars, overlapped by fourth supraocular and palpebrals, and overlapping postsuboculars; postsupraocular overlapped by fourth supraocular and postoculars, and overlapping parietal and primary temporal; postsuboculars four, smooth, first one overlapped by fourth supralabial, and overlapping fifth supralabial; temporals in seven rows, those in secondary and tertiary rows more or less enlarged, uppermost secondary temporal divided, overlapped by parietal together with uppermost tertiary temporal; temporals in the other rows subequal to body scales in size; tympanum superficial; mental overlapping first infralabials and postmental; postmental undivided, overlapped by mental and first infralabials, and overlapping first chinshields; chinshields in three pairs, first right one overlapped by first left one, second pair separated by single scale, third pair separated by three scales; five infralabials; one scale broadly overlapping third left chinshield, and

FIG. 8. Male (A) and female (B) *Tropidophorus murphyi* sp. nov. in life. Note relatively broad body in the latter.

overlapped by fourth and fifth infralabials; 30 midbody scale rows; 13 scale rows at position of tenth subcaudal on tail; paravertebrals 62, subequal in size to neighboring scales, smooth or feebly keeled on neck, body, and base of tail, and moderately keeled on

the remaining portion of tail; scales in row adjacent to paravertebral row on each side weakly keeled on neck, body and tail; dorsolateral and lateral scales distinctly keeled; six rows of mid-ventral scales smooth, scales in outer row on each side feebly keeled; preanals two, enlarged, right one overlapped by left one; subcaudals smooth, four times as broad as neighboring scales, remaining ones only two times as broad as neighboring keeled scales; scales on ventral surfaces of hindlimbs only feebly keeled, those on the other portions of hindlimbs and on forelimbs distinctly keeled; 24 subdigitals on fourth toe. Presacral vertebrae 26.

Left testis 4.7 mm in longer axis.

Measurements of holotype (mm)

SVL, 85.1; tail length, 101.0 (tail tip lost); snout to forelimb length, 30.5; head length, 14.3; head width, 12.3; head depth, 6.4; snout length, 5.7; eye length, 5.0; eye to tympanum length, 6.5; snout to tympanum length, 16.7; tympanum height, 3.1; tympanum width, 2.3; axila to groin length, 42.8; midbody width, 14.7; midbody depth, 5.5; forelimb length, 22.9; hindlimb length, 33.0; fourth toe length 11.7.

Color in preservative

Dark brown or dorsal and lateral surfaces of head, body, and tail; three, seven, and 17 transverse bands, pale brown in color and rather irregular in shape, on dorsal surfaces of neck, body, and tail, respectively; several pale brown spots on supralabials and infralabials; yellowish ivory on gular and venter; ventral surface of tail yellowish ivory with indistinct dark flecks.

Variation

Of paratypes, three adult males and one young male measured 62.4–85.1 mm and 55.2 mm in SVL, respectively, while SVL in five adult and two immature females ranged from 92.2 to 96.3 and from 56.1 to 76.8, respectively. Relative breadth of body was distinctly greater in adult females than in adult males (midbody width/SVL*100: 18.6–22.0, vs. 17.7–18.2) (Fig. 8). The paravetebral number was also greater in females than in males (mean and range: 59.6 and 60–67, vs 62.6 and 55–62). No intersexual differences were evident in other scale characters. The number of midbody scale rows ranged from 30 to 32. Upper and lower anterior loreals were fused on one side in two specimens and on both sides in one specimen. The arrangement of nuchals was highly variable, two on both sides in five specimens, none on both sides in two specimens, two on left and three on right in two specimens, two on left and none on right in one specimen, two on left and four on right in one specimen, and three on both sides in one specimen. Supralabials were invariably six. Infralabials were usually five, but rarely six. Superciliaries were usually six or seven, but rarely five or eight. Frontal contacted usually two, but rarely three supraoculars. The number of subdigitals ranged from 20 to 25. Scale rows on tail at position of tenth subcaudal were invariably 13.

Etymology

The name is dedicated to Dr. Robert W. Murphy of the Royal Ontario Museum, the project leader of the herpetological survey in Vietnam, during which the present species was discovered.

Natural history

All specimens were collected in humid rocky areas along a stream flanked by steep rocky slopes with bush. There were many moist crevices in the rocks, in which the skinks hid themselves during the daytime. Active individuals were observed only after sunset, and this strongly suggests that this species is nocturnal. Because individuals, prevented from direct contact with moist substrates, showed rapid dehydration even under high atmospheric humidity, it is likely that *T. murphyi* is highly vulnerable to drought. Another congeneric species, *T. sinicus* occurred sympatrically, but was found under

rocks closer to the stream.

Female paratypes had 3–5 eggs in oviducts, which had no recognizable embryos. A non-type female from the type locality, kept in captivity at Tula Exotarium, Russia, gave birth to a juvenile, 28 mm in SVL, on 30 March 2002. It is thus obvious that this species is viviparous like several other congeneric species (Smith, 1923; Taylor, 1963).

Discussion

Smith (1923), in a revision of the genus *Tropidophorus* from the continental region of Southeast Asia, recognized nine species. Later, *T. baviensis* and *T. guanxiensis* were described from northern Vietnam, and Guanxi, China, respectively (Bourret, 1939; Wen, 1992), making the total number of recognized continental species of *Tropidophorus* 11. Of these, *T. baviensis* most resembles *T. latiscutatus*, *T. matsuii*, and *T. murphyi* in having keeled scales on the temporal and smooth scales on the remaining dorsal and lateral surfaces of the head, and smooth or feebly keeled dorsal scales on the body. These three species, however, differ from *T. baviensis* or any other congeneric species so far described in having a distinctly depressed body. Moreover, the numbers of paravertebrals in the present species are distinctly greater than that in *T. baviensis* (Table 1).

Of the three depressed-bodied species described above, the degree of depression, particularly of the head, is much greater in *T, murphyi* than in the two Thailand species (Table 1, Fig. 9). *Tropidophorus matsuii* differs from *T. latiscutatus* in having greater numbers of midbody scale rows and paravertebrals. Also, *T. matsuii* is distinct from *T. latiscutatus*, as well as from *T. murphyi* and *T. baviensis*, in having a divided frontonasal. *Tropidophorus latiscutatus* is distinct from the other species in having distinctly widened paravertebrals (Table 1).

Species characterized by distinctly depressed bodies have been reported for a few other lizard families, such as Gekkonidae, Iguanidae, and Xenosauridae. Because many of these species are strongly associated with saxi-

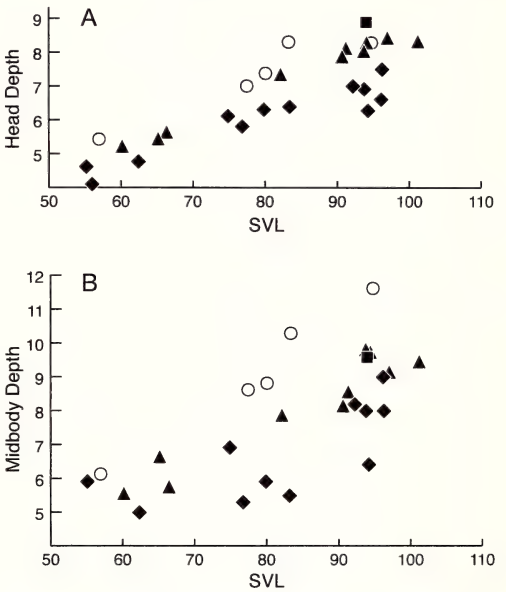

FIG. 9. Two dimensional plots of head depth (A) and depth at midbody (B) against snout-vent length (SVL), showing interspecific variations in degrees of head and body depressions, respectively. See Fig. 1 for explanations of symbols.

TABLE 1. Comparisons in external characters of the three depressed-bodied *Tropidophorus* and *T. baviensis*.

Character	*T. baviensis*	*T. latiscutatus*	*T. matsuii*	*T. murphyi*
Body depression	slight	moderate	moderate	extreme
Midbody scale rows	28–30	28–30	34	30–32
Frontonasal	undivided	undivided	divided	undivided
Paravertebral widened	no	yes	no	no
Paravertebral number	49–53	58–63	65	59–67

colous habitats, such body depression is often regarded as a kind of adaptation to the use of narrow rock crevices as shelters for predatory avoidance (Vitt, 1981; Doughty and Shine, 1995; Ballinger et al., 2000). Known members of the genus *Tropidophorus*, including *T. baviensis*, are usually found beneath rocks and leaf litter on the forest floor (occasionally close to a stream: Taylor, 1963; Brown and Alcala, 1980), or in burrows on banks (*T. baviensis*: Ngo et al., 2000). Discovery of the three exceptionally depressed-bodied *Tropidophorus* in rock crevices, a type of habitat also exceptional to the genus, offers a first substantial support from the Scincidae for the assumption regarding the enhancement of body depression by this type of habitat.

Several authors have assumed that in lizards the physical constraint from the crevice-dwelling habits provides an evolutionary force to some reproductive traits, such as relative clutch mass and frequency of clutch production (Vitt, 1981, 1993; Doughty and Shine, 1995). However, relevant hypotheses have not yet been sufficiently assessed by appropriate comparative approaches (e.g., see Ballinger et al. [2000]). The present species and *T. baviensis*, seemingly representing differential stages of an adaptation to life in rock crevices, would offer a good opportunity to examine the evolutionary consequences of crevice-dwelling habits in reproductive and other ecological and physiological traits.

Acknowledgments

T. Hikida and H. Ota thank M. Matsui for providing opportunities to visit Thailand, and S. Panha, M. Matsui, K. Araya, M. Toda, T. Chen, and M. Honda for helping with field work there. Likewise, N. L. Orlov is very grateful to R. W. Murphy for enabling him to make field surveys in Vietnam, and to A. Lathrop, T. Mason, Ho Thu Cuc, Nguyen Van Sang, S. Ryabov, and E. Rybaltovsky for their assistance during the field work. We are also much indebted to I. Ineich and A. Dubois (MNHN) for allowing us to examine the type specimen of *T. baviensis* under their care, to M. Hori for facilities for autoradiography, to S. Sakata for helping with preparations of line drawings and radiographs, and to N. B. Ananjeva for various help in preparing the draft of this manuscript.

Sampling of lizards in Thailand was carried out with the permission of the National Research Council of Thailand (NRCT), Bangkok, and with financial support from a Monbusho International Scientific Program (Field Research No. 08041144; project leader: M. Matsui). For the Vietnamese specimens, permission for collecting and exporting was obtained from the Vietnam Institute of Ecology and Biological Resource (IEBR), Hanoi.

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APPENDIX

Specimens examined for comparisons

See text for institutional acronyms.

Tropidophorus baviensis.—MNHN 1948.63 (holotype), Mt. Ba Vi, Ha Tay Province, northern Vietnam; ZISP 22251 (N-37), Ba Vi National Park, Ha Tay Province, northern Vietnam; ZISP 19805, Cuc Phuong National Park, Hoa Binh Province, northern Vietnam; ZISP 21009-1, 21009-2, Myiongte, Lai Chau Province, northern Vietnam.

Accepted: 28 May 2002

Current Herpetology 21(1): 25–34, June 2002

Taxonomic Relationships of an Endangered Japanese Salamander *Hynobius hidamontanus* Matsui, 1987 with *H. tenuis* Nambu, 1991 (Amphibia: Caudata)

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Abstract: We assessed the taxonomic relationships of an endangered Japanese small salamander, *Hynobius hidamontanus* Matsui, 1987, and its close relative *H. tenuis* Nambu, 1991 electrophoretically and found that they were not clearly distinguished from each other. This result, together with available morphological and ecological information, strongly indicates that *H. tenuis* Nambu, 1991 is a subjective junior synonym of *H. hidamontanus* Matsui, 1987. By this conclusion, the total distribution range of *H. hidamontanus* is greatly expanded, but its endangered status and the necessity of its conservation is not be changed since the habitats of this species are fragmented and not continuous. The distribution pattern of this species is interesting from the viewpoint of biogeography.

Key words: Hynobiidae; Allozyme; Specific status; Conservation; Biogeography; Japan

INTRODUCTION

Reliable taxonomic identification of animals forms a fundamental basis for estimating species richness, which forms the most important basis in conserving animal biodiversity (May, 1995). Through the use of biochemical techniques, the presence of many new species has been elucidated in various animals, and this has rapidly increased the known species diversity of animals including amphibians (e.g., Glaw et al., 1998).

Pertinent taxonomic identification of populations of a species also affects appropriate measures of conservational and protective status of each species. Currently, species formerly considered to be widespread in their distribution and omitted from "Red List" tend to be split into several distinct species, and each of these needs new conservation measures because of its more restricted range of distribution (e.g., Nishikawa et al., 2001).

However, though the number of cases is fewer, more than one species hitherto considered to be distinct from others has been

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proven to be identical to another species through extensive biochemical studies. We herewith report such a case found in two species of Japanese hynobiid salamanders.

Matsui (1987) described a salamander, *H. hidamontanus*, from a montane region of Nagano Prefecture, central Honshu, mainland of Japan, on the basis of morphological and biochemical evidence. The species was later listed as an endangered species in IUCN (IUCN, 1996) and Japanese (Matsui, 2000a) Red Data Books. On the other hand, Nambu (1983) reported the occurrence of hynobiid salamanders from montane regions of Toyama and Niigata Prefectures, surrounding Nagano. Although Matsui (1987: 62) pointed out that these salamanders share diagnostic characteristics with *H. hidamontanus*, Nambu (1991) described them as a separate species, *H. tenuis*, on the basis of a specimen from Arimine, Ooyama-machi, Toyama Prefecture. Nambu (1991), while also considering this species to be closely related to *H. hidamontanus* Matsui, 1987 in sharing several morphological characteristics, such as the lack of the fifth toe, the small number of vomerine teeth, and similar body proportions, argued for its difference from the latter in skull morphology (Nambu, 1991: 995).

Nambu (1991), however, did not make any quantitative analyses such as statistical comparisons of morphological characteristics using a large number of specimens or electrophoretic assessment of genetic differentiation, both of which are routine in the taxonomic study of hynobiid salamanders (e.g., Matsui and Miyazaki, 1984; Matsui, 1987; Matsui et al., 1992).

The taxonomic validity of *H. tenuis*, therefore, remains dubious (Matsui, 1996b, 2000a), but no study has been conducted to reassess the taxonomic relationship of this species and *H. hidamontanus*. Because, as noted above, *H. hidamontanus* is now considered to be endangered (IUCN, 1996; Matsui, 2000a), elucidation of the taxonomic relationships of *H. tenuis* and *H. hidamontanus* has become urgent from the viewpoint of species conservation.

Small salamanders of the genus *Hynobius* exhibit high inter- and intraspecific variations in morphology, and, therefore, species identification is usually difficult without locality information (Matsui and Miyazaki, 1984). For studies of intra- and interspecific variations and taxonomy among morphologically similar urodelan species, electrophoretic studies contribute the best data (e.g., Matsui et al., 1992, 2000; Jackman and Wake, 1994; Highton, 1999). Indeed, recent genetic analyses by electrophoresis have elucidated many taxonomic problems in *Hynobius* (e.g., Matsui 1987; Nishikawa et al., 2001). Herein, we examined the taxonomic validity of *H. tenuis* chiefly by means of this technique.

Materials and Methods

The small Japanese salamanders generally occur allopatrically (Matsui, 1996a), and only one species has been recorded from each of the type localities of *H. hidamontanus* and *H. tenuis* (Matsui, 1996b). Therefore, there is little possibility that samples collected from each of these localities will include more than one species. In addition to this, *H. hidamontanus* closely resembles *H. lichenatus* in external morphology (Matsui and Matsui, 1980), but is reported to form a genetic group not with the latter but with *H. nebulosus* (Matsui, 1987). We therefore used both *H. lichenatus* and *H. nebulosus* for comparisons. Further, because populations of many small Japanese salamanders are in decline (Matsui, 2000a), we need to refrain from collecting a large number of specimens. Bearing this in mind, we used a total of 46 specimens to evaluate genetic relationships among four species: *H. tenuis* from Toyama (sample 1, topotypic population, N=13), and Gifu (sample 2, N=7) Prefectures, *H. hidamontanus* from Nagano Prefecture (sample 3, topotypic population, N=16), and one population each of *H. nebulosus* from Shiga Prefecture (sample 4, N=4) and *H. lichenatus*

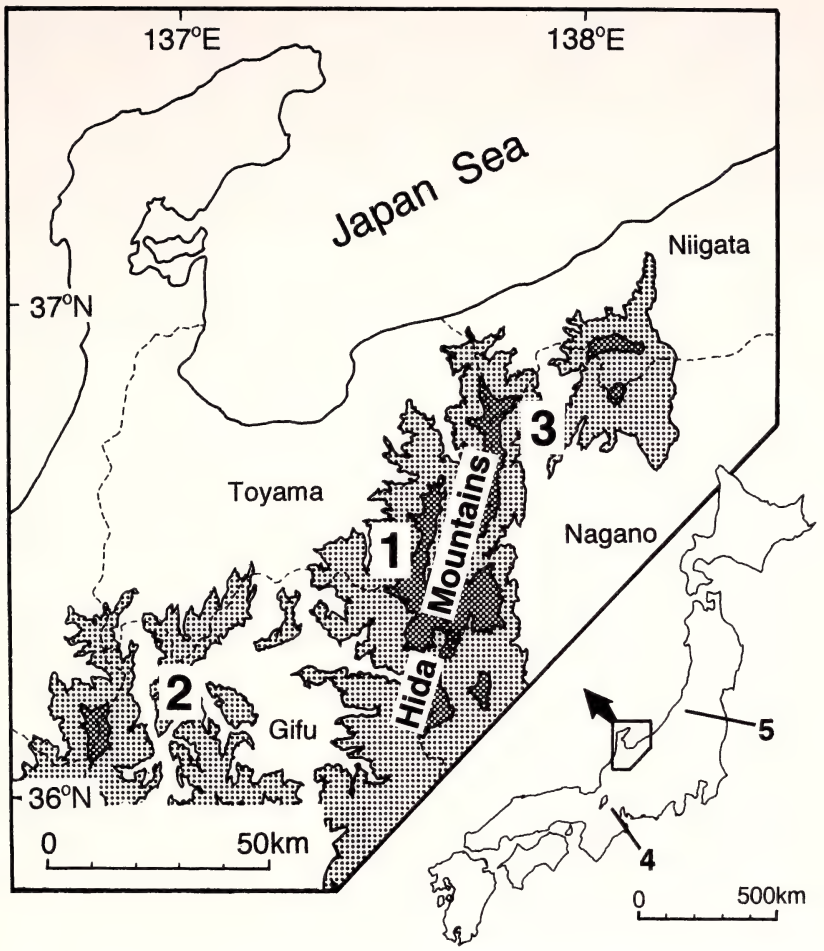

FIG. 1. A map of northern Central Honshu, Japan, showing sampled localities of hynobiid species used in this study. For sample numbers, refer to text. Coarsely dotted area >1000 m asl. Finely dotted area >2000 m asl.

from Yamagata Prefecture (sample 5, N=6) (Fig. 1).

In the laboratory, liver samples were removed from fully anesthetized salamanders and stored at -84 C. Voucher specimens were fixed in 10% formalin, preserved in 70% ethanol, and deposited in the Graduate School of Human and Environmental Studies, Kyoto University (KUHE) (see Appendix). Supernate fraction and homogenates were examined by standard horizontal starch gel electrophoresis (Shaw and Prasad, 1970; Ayala et al., 1972), containing Starch Art (Starch Art Corp., Smithville, USA) and Connaught starch (Connaught Lab., Ontario, Canada) mixed in a 4:1 ratio and then suspended in buffer at a concentration of 11.5%. Enzymes examined, locus designations, and buffer systems employed are listed in Table 1. Staining methods, genetic interpretations of allozyme data, enzyme nomenclature, E. C. numbers, abbreviations, and isozyme designations follow Nishikawa et al. (2001).

We studied 19 enzyme systems coded by 24 presumptive loci (Table 1). Genetic variability for each sample was assessed by the standard analyses: percentage loci polymorphic (P, a locus is considered as polymorphic unless the frequency of the most common allele exceeds 0.95), the mean heterozygosity

TABLE 1. Enzymes, presumptive loci, and buffer systems used in the analyses of allozyme variations among *Hynobius* species.

Enzymes	E.C. numbers	Locus	Buffer system*
Aconitate hydratase	4.2.1.3	mAcoh-A	TC8
Aspartate aminotransferase	2.6.1.1	mAat-A	CAPM6
Aspartate aminotransferase	2.6.1.1	sAat-A	CAPM6, TC7
Alcohol dehydrogenase	1.1.1.1	Adh-A	TBE8.7
Fumarate hydratase	4.2.1.1	Fumh-A	TBE8.7
Glucose-6-phosphate isomerase	5.3.1.9	Gpi-A	CAPM6
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3pdh-A	TC8
Glutamate dehydrogenase	1.4.1.3	Gtdh-A	TC8
Guanine deamidase	3.5.4.3	Gda-A	TBE8.7
3-Hydroxybuthyrate dehydrogenase	1.1.1.30	Hbdh-A	CAPM6
Isocitrate dehydrogenase	1.1.1.42	mIdh-A	TC7
L-Lactate dehydrogenase	1.1.1.27	Ldh-A	CAPM6, TC7
L-Lactate dehydrogenase	1.1.1.27	Ldh-B	CAPM6, TC7
Malate dehydrogenase	1.1.1.37	mMdh-A	CAPM6, TC8
Malate dehydrogenase	1.1.1.37	sMdh-A	CAPM6, TC8
Malic enzyme**	1.1.1.40	mMdhp-A	TC7
Malic enzyme**	1.1.1.40	sMdhp-A	TC7
Peptidase (leucyl-glycine)	3.4.11.-	Pep-A	TBE8.7
Phosphoglucomutase	5.4.2.2	Pgm-A	TC7
Phosphoglucomutase	5.4.2.2	Pgm-C	TC7
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh-A	TC7
Sorbitol dehydrogenase	1.1.1.14	Sdh-A	CAPM6
Superoxide dismutase	1.15.1.1	Sod-A	TBE8.7
Xanthine dehydrogenase	1.1.1.204	Xdh-A	TC8

* Buffer systems—CAPM6: Citrate-aminopropylmorpholine, pH=6.0 (Clayton and Tretiak, 1972), TC7: Tris-citrate, pH=7.0 (Shaw and Prasad, 1970), TC8: Tris-citrate, pH=8.0 (Clayton and Tretiak, 1972), TBE8.7: Tris-borate-EDTA, pH=8.7 (Boyer et al., 1963).

** NADP-dependent malate dehydrogenase.

by direct count (H), and the mean number of electromorphs per locus (A).

In order to estimate overall genetic divergence among samples, we calculated two genetic distances: Nei's (1978) unbiased genetic distance and modified Rogers' distance (Wright, 1978). We inferred patterns of phenetic similarities among samples from Nei's (1978) distance clustered by the UPGMA algorithm (Sneath and Sokal, 1973), and modified Rogers' distance clustered by the Neighbor-joining (NJ) procedure (Saitou and Nei, 1987). *Hynobius lichenatus* (sample 5) was designated as an outgroup in the NJ method.

We ran these analyses by employing BIOSYS-1 (Swofford and Selander, 1981) and PHYLIP vers. 3.5 C computer programs (Felsenstein, 1993).

RESULTS

Fifty-two alleles were detected at 24 putative loci of which 16 (other than mAat-A, mAcoh-A, Fumh-A, Gtdh-A, sMdhp-A, Pgm-A, Sdh-A, and Sod-A) were variable (Table 2). The most variable loci were Gda-A,

Gpi-A, and Pgdh-A, each with four alleles, followed by Adh-A, G3pdh-A, mIdh-A, Ldh-B, sMdh-A, and Xdh-A, each with three alleles. Adh-A in *H. nebulosus*, and sAat-A, Adh-A, Hbdh-A, and sMdh-A in *H. lichenatus* were fixed by unique alleles that were not shared with other species. We found no unique alleles in either *H. tenuis* or *H. hidamontanus*. However, we found some differentiations of allelic frequencies in Gda-A, Gpi-A, and Ldh-A, among *H. tenuis* and *H. hidamontanus* (samples 1–3).

The mean number of electromorphs per locus (A) varied from 1.1 to 1.3, the percentage of polymorphic loci (P) from 4.2 to 25.0, and the mean heterozygosity (H) from

TABLE 2. Allele frequencies at 16 polymorphic loci of *Hynobius* samples examined. For sample numbers, refer to Fig. 1 and text. A=mean number of alleles per locus; P=percentage of loci; H=mean heterozygosity by direct count.

	Species and sample number (N)				
	tenuis	*tenuis*	*hidamontanus*	*nebulosus*	*lichenatus*
Locus	1 (13)	2 (7)	3 (16)	4 (4)	5 (6)
sAat-A	a1.000	a1.000	a1.000	a1.000	b1.000
Adh-A	a1.000	a1.000	a1.000	c1.000	b1.000
Gda-A	a0.923	a0.143	a1.000	b1.000	b1.000
	d0.077	c0.429			
		d0.429			
G3pdh-A	b1.000	b1.000	a0.063	c1.000	c1.000
			b0.938		
Gpi-A	b0.462	b1.000	b1.000	a0.375	b0.833
	c0.192			c0.500	d0.167
	d0.346			d0.125	
Hbdh-A	a1.000	a1.000	a1.000	a1.000	b1.000
mIdh-A	a0.962	a1.000	a1.000	a0.500	a0.833
	b0.038			c0.500	b0.167
Ldh-A	a0.077	a1.000	b1.000	a1.000	b1.000
	b0.923				
Ldh-B	c1.000	c1.000	c1.000	a0.500	c1.000
				b0.500	
mMdh-A	b1.000	b1.000	b1.000	b1.000	a0.167
					b0.833
sMdh-A	c1.000	c1.000	c1.000	a0.250	b1.000
				c0.750	
mMdhp-A	b1.000	b1.000	b1.000	b1.000	a0.167
					b0.833
Pep-A	b1.000	b1.000	b1.000	a1.000	a1.000
Pgdh-A	c1.000	c1.000	c1.000	a1.000	a0.083
					b0.083
					c0.083
					d0.750
Pgm-C	a1.000	a1.000	a0.938	a0.125	a1.000
			b0.063	b0.875	
Xdh-A	a0.923	a1.000	a0.969	a0.750	a1.000
	c0.077		b0.031	c0.250	
A	1.3	1.1	1.1	1.3	1.3
P	16.4	4.2	8.3	25.0	20.8
H	0.010	0.000	0.003	0.031	0.021

0.00 to 0.03 (Table 2). The highest A, P, and H values were found in *H. nebulosus* (sample 4), while the lowest A value was seen in *H. tenuis* from Gifu Prefecture (sample 2) and *H. hidamontanus* (sample 3), and the lowest P and H values were shown by *H. tenuis* from Gifu Prefecture (sample 2).

As shown in Table 3, the highest Nei's (1978) and modified Rogers' distances were obtained between *H. tenuis* (sample 2) and *H. lichenatus* (sample 5) (0.46 and 0.60, respectively). By contrast, the lowest distances were found between *H. tenuis* from Toyama Prefecture (sample 1) and *H. hidamontanus* (sample 3) (0.01 and 0.10, respectively).

Results of UPGMA and NJ analyses are shown in Fig. 2. In both phenograms, *H. tenuis* from Toyama Prefecture (sample 1) joined with *H. hidamontanus* (sample 3) first, and then with *H. tenuis* from Gifu Prefecture (sample 2): the two populations of *H. tenuis* were not clustered as one group. In the UPGMA tree, relationships among the three groups, the *tenuis-hidamontanus* group, *H. nebulosus* (sample 4), and *H. lichenatus* (sample 5) were not solved clearly, but distances among them were substantially large.

TABLE 3. Matrix of Nei's (1978) unbiased genetic distance (above diagonal) and modified Rogers' distance (Wright, 1978: below diagonal). Diagonal numbers show the numbers of loci fixed by unique allele(s).

Samples	1	2	3	4	5
1	0	0.067	0.009	0.429	0.419
2	0.253	0	0.067	0.383	0.460
3	0.102	0.255	0	0.457	0.406
4	0.573	0.551	0.592	1	0.433
5	0.571	0.596	0.569	0.573	4

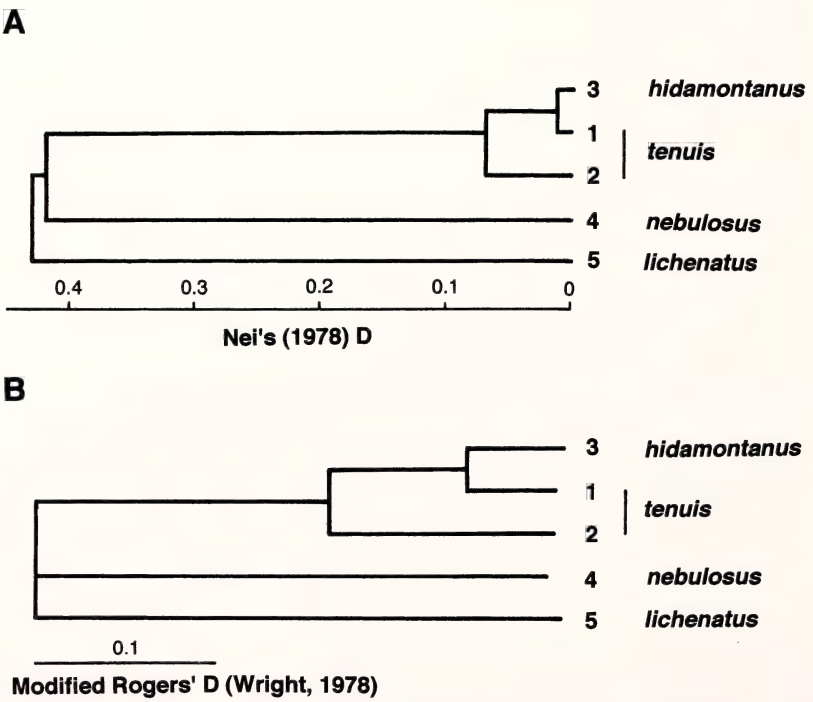

FIG. 2. UPGMA tree based on Nei's (1978) unbiased genetic distances (A) and an NJ tree based on modified Rogers distances (Wright, 1978) rooted by the outgroup (sample 5) (B), among five samples studied. For sample numbers, refer to text.

Discussion

Recent biochemical reassessments of the Japanese small salamanders have resulted in elucidating the presence within a named species of many genetically distinct populations that require taxonomic splitting (cf. Matsui, 2000b). However, the present biochemical study of *H. hidamontanus* and *H. tenuis* has provided an opposite conclusion, i.e., the two species are genetically conspecific.

As shown by the values of A, P, and H, each sample of *H. hidamontanus* and *H. tenuis* did not exhibit particularly great genetic differentiation within a locality, and so there was little possibility of there being a mixture of more than one species. The topotypic populations of *H. tenuis* from Toyama and *H. hidamontanus* from Nagano Prefectures first formed a group with the smallest genetic distance (Nei's D=0.01) among all pairs compared, and the other population of *H. tenuis* from Gifu Prefecture had a sister relationship to this group. This very small genetic differentiation between the topotypic populations offers little support for taxonomic separation of these two species.

Matsui (1987) reported the Nei's (1978) D between *H. hidamontanus* and *H. nebulosus* to be 0.30, which value is smaller than what we found in this study (0.46), notwithstanding the use of the same populations in the two studies. This discordance might have been induced by differences in specimens used, number of loci examined, and the electrophoretic conditions, especially the larger number of buffer systems employed in this study which might have separated more electromorphs. In this way, the absolute genetic distances derived from allozymic data themselves are variable, and were not directly used for outlining species boundaries. Relative distances from allozymic data, however, show a good taxonomic standard (Matsui, 2000b). *Hynobius tenuis* and *H. hidamontanus* are genetically not considered to be different species because their genetic distances are much smaller than are found among already named species or even within one species of *Hynobius* (D>0.22: e.g., Matsui 1987; Matsui et al. 2000; Nishikawa et al. 2001).

Allelic compositions of Gda-A, Gpi-A, and Ldh-A show some genetic fragmentation among *H. tenuis* and *H. hidamontanus* (samples 1–3). Matsui (1987) already reported genetic variations in *H. hidamontanus*. Namely, he found fixed differences in two loci and Nei's (1978) D of 0.20 between two populations of this species. However, he treated them as one species because of their morphological similarities.

Nambu (1991) argued that *H. tenuis* is specifically distinct from *H. hidamontanus* on the basis of different conditions in five skull characters (angle of articulation of maxilla and premaxilla, length and shape of maxilla, shape of premaxilla, shape of vomer, and proportion of vomerine teeth series). However, the skull morphology sometimes greatly varies even within a single species in *Hynobius* salamanders (Ebitani, 1952).

Our preliminary examinations of morphological variations in *H. tenuis* and *H. hidamontanus* specimens including those from their type localities revealed the absence of tangible differences in these two species (Matsui, 1996b; Matsui et al., unpublished data). In addition to these morphological similarities, descriptions in the literature (Matsui and Matsui, 1980; Nambu, 1983) and our extensive ecological observations in the field strongly indicate that they live and spawn in very similar habitats (slowly flowing water in marshes and swamps near montane forests), and share a similar ecological niche.

From these lines of evidence, we have no other choice but to conclude that *H. tenuis* Nambu, 1991, is a subjective junior synonym of *H. hidamontanus* Matsui, 1987, and that separation of the two species even at the subspecific level is not necessary. Although no further studies have been made, the population of a salamander from O-umi, Niigata Prefecture (Matsui, 1987) should also be included in this species from its diagnostic characteristics (see Matsui, 1987: 62).

A case similar to that reported in the present paper has been known in some plethodontid salamanders; Feder et al. (1978) found little allozymic variation between *Plethodon dunni* and *P. gordoni* and also found that none of the diagnostic characters mentioned in the original description of *P. gordoni* were reliable. Consequently, they (Feder et al., 1978) synonymized *P. gordoni* as a color variant of *P. dunni*.

The discovery of *H. hidamontanus* (Matsui and Matsui, 1980; Matsui, 1987) and *H. tenuis* (Nambu, 1983, 1991) filled the distributional gaps of lentic breeding salamanders known previously (Sato, 1943; Nakamura and Uéno, 1963; Matsui and Miyazaki, 1984). The geohistory of the Japanese islands including the formation of the Fossa Magna (=Itoigawa-Shizuoka tectonic line) was supposed to have strongly affected the formation of patterns in distribution and divergence of these animals (Matsui, 1987; Matsui et al., 2000; Nishikawa et al., 2001).

Until now, the high montane region of the Hida Mountains could be considered a geographic barrier that had promoted the divergence of *H. hidamontanus* and *H. tenuis*, occurring on its eastern and western sides, respectively. The close genetic similarities demonstrated in the present study, however, indicate the invasion either (1) from west of the population ancestral to the present eastern population (*H. hidamontanus* sensu stricto), or (2) from east of the ancestral population of the present western population (*H. tenuis*), possibly through a route north of the northernmost edge of the Hida Mountains.

The relationships among *H. hidamontanus* (sensu lato), *H. nebulosus*, and *H. lichenatus* were not clearly resolved in the present study, but through the use of more extensive samples, Matsui (1987) considered that *H. hidamontanus* belongs to one of the two large lineages of Japanese lentic breeding *Hynobius* and is phylogenetically closer to *H. nebulosus* from western Japan than to the eastern lineage including *H. lichenatus*. If this is the case, the first hypothesis advanced above seems more plausible. *Hynobius hidamontanus* (now including *H. tenuis*) occurs on the western side of the Fossa Magna and *H. lichenatus* occupies its eastern side (Matsui, 1987). If these two species actually belong to different lineages, as stated above, the possible dichotomy in the lentic breeding *Hynobius* in older times might have prevented further eastwards invasion of *H. hidamontanus*.

The present results greatly expand the range of distribution of *H. hidamontanus*, which was formerly limited to around the type locality in Hakuba Village, Nagano Prefecture (Matsui, 1987, 2000a). The species (sensu stricto) has been listed in Red Data Books for the reason that its habitats are limited and being destroyed (IUCN, 1996; Matsui, 2000a). We need to maintain this conservational status of *H. hidamontanus* because, even after synonymizing *H. tenuis* with it, the actual habitats, though ranging over a seemingly large area, are largely isolated from each other and the size of each local population is obviously very small (Matsui, 2001: 198).

Acknowledgments

We would like to thank T. Abe and S. Tanabe for help in collecting the specimens examined. This work was supported by Grants-in-Aid to MM (No. 11640697) from the Ministry of Education, Science, Sports and Culture, Japan, through the Japan Society for the Promotion of Science and a grant from the Environment Agency of Japan (now the Ministry of Environment).

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APPENDIX

Materials examined

Voucher specimens used for electrophoresis are stored at the Graduate School of Human and Environmental Studies, Kyoto University (KUHE).

Sample 1: *Hynobius tenuis* from Ooyama-machi, Toyama Prefecture (KUHE 13236–13248).

Sample 2: *H. tenuis* from Shirakawa-mura, Gifu Prefecture (KUHE 13262–13263, 13265–13269).

Sample 3: *H. hidamontanus* from Hakuba-mura, Nagano Prefecture (KUHE 9481, 9484–9485, 9498–9510).

Sample 4: *H. nebulosus* from Hino-cho, Shiga Prefecture (KUHE 9599–9600, 16937–16938).

Sample 5: *H. lichenatus* from Oguni-cho, Yamagata Prefecture (KUHE 18421, 18426–18427, 18432, 18436–18437).

Accepted: 29 May 2002

Current Herpetology 21(1): 35–41, June 2002

Karyotypes of Four Agamid Lizards from Southeast Asia

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Abstract: We karyotyped four lizards, *Acanthosaura armata*, *Bronchocela cristatella*, *Calotes emma*, and *C. versicolor*, all belonging to the tropical Asian clade of the family Agamidae. The karyotype of *A. armata* consisted of 12 metacentric macrochromosomes and 20 microchromosomes, whereas *B. cristatella* had 14 metacentric macrochromosomes and 20 microchromosomes. Except for the presence of 22 microchromosomes, the karyotypes of the two *Calotes* species were similar to that of *A. armata*. The 20 microchromosome state in the *A. armata* karyotype may have emerged in the ancestral lineage common to *Gonocephalus robinsonii*, whose karyotype also exhibits a 12M + 20m format. Comparison of the present results with previously published information suggests the presence of cryptic taxonomic diversity in *B. cristatella* and *C. versicolor*.

Key words: Karyotype; Chromosomal variation; Agamidae; *Acanthosaura armata*; *Bronchocela cristatella*; *Calotes emma*; *C. versicolor*; Southeast Asia.

INTRODUCTION

The family Agamidae is an Old-World representative of the iguanian lizards, and is much diverged in Australia, Africa, tropical and temperate Asia, and the Indo-Australian Archipelago. Recent molecular studies yielded a few tenable hypotheses for early stages of divergence in this family (Honda et al., 2000; Macey et al., 2000). With respect to the phylogeny and systematics at generic and infrageneric levels, however, much is yet to be done for the Agamidae.

Chromosomal approaches to phylogeny have been receiving persistent, formidable criticism chiefly on the ground of adequacy in analytical procedures adopted and in presumptions regarding the mode and direction of character transformation (e.g., Kluge, 1994). In some cases, however, chromosomal data have been providing very convincing evidence for monophyly in some agamid groups (e.g., Diong et al.,

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2000; Honda et al., 2002). Also, chromosomal investigation may clarify biological species that are cryptic to morphological approaches (King, 1993: see Ota [1988] for example of an agamid group).

In consideration of these merits, we have been conducting a chromosomal survey of Southeast Asian agamid lizards (Diong et al., 2000). In this paper, we describe karyotypes of four species obtained in this survey.

Materials and Methods

A total of 16 specimens representing four species, *Acanthosaura armata, Bronchocella cristatela, Calotes emma*, and *C. versicolor*, were karyotyped (Table 1). All of these species belong to group V of the Agamidae sensu Moody (1980) (see Honda et al. [2000, 2002] and Macey et al. [2000: as the South Asian clade] for the monophyly of this group).

Mitotic cell preparations were made by the bone-marrow air-dry method following Diong et al. (2000). Then they were stained in 6% Gurr Giemsa (BDH) solution, and were photographed with a Nikon Optiphot 2 Photomicrography camera using Kodak TMAX ASA 100 film.

Karyotypes were determined for each individual lizard on the basis of 10–16 well-spread metaphase cells. Chromosomes in each photograph were paired according to the similarity in size and shape, and resultant pairs were arranged in order of decreasing size. For the calculation of arm ratio for each chromosome pair, the lengths of chromosome arms were measured with a CALCOM digitizer. Terminology for chromosomal description follows Levan et al. (1964) as modified by Green and Sessions (1991), and the karyotype formula follows Peccinini-Seale (1981). Voucher specimens were deposited in the Zoological Reference Collection, Department of Biological Sciences, National University of Singapore (ZRC).

Results

The karyotype of male *Acanthosaura armata* consisted of 16 pairs. Of these, the six largest pairs were all metacentric macrochromosomes, and the remaining 10 were microchromosomes (Fig. 1A). Fundamental numbers (N. F.) thus equaled 44. In the macrochromosome group, there was a marked size gap between pairs 5 and 6 (also see Appendix).

The karyotype of male *Bronchocela cristatella* was similar to that of *A. armata* in the clear division of component chromosomes into metacentric macrochromosomes and microchromosomes. However, the macrochromosome group of the *B. cristatella* karyotype had an additional pair, which made its diploid and fundamental numbers 34 and 48, respectively (Fig. 1B). Also, the karyotype of *B. cristatella* differed from that of *A. armata* in the presence of a distinct size gap between pairs 1 and 2, besides between pairs 5 and 6 (Fig. 1B, Appendix).

Table 1. Localities, sizes, and sexual composition of samples of four agamid species examined in this study.

Species	N			Locality
	Males	Females	Total	
Acanthosaura armata	3	0	3	Pulau Tioman, near Peninsular Malaysia
Bronchocela cristatella	4	0	4	Singapore
Calotes emma	1	0	1	Banding, Peninsular Malaysia
Calotes versicolor	5	3	8	Singapore

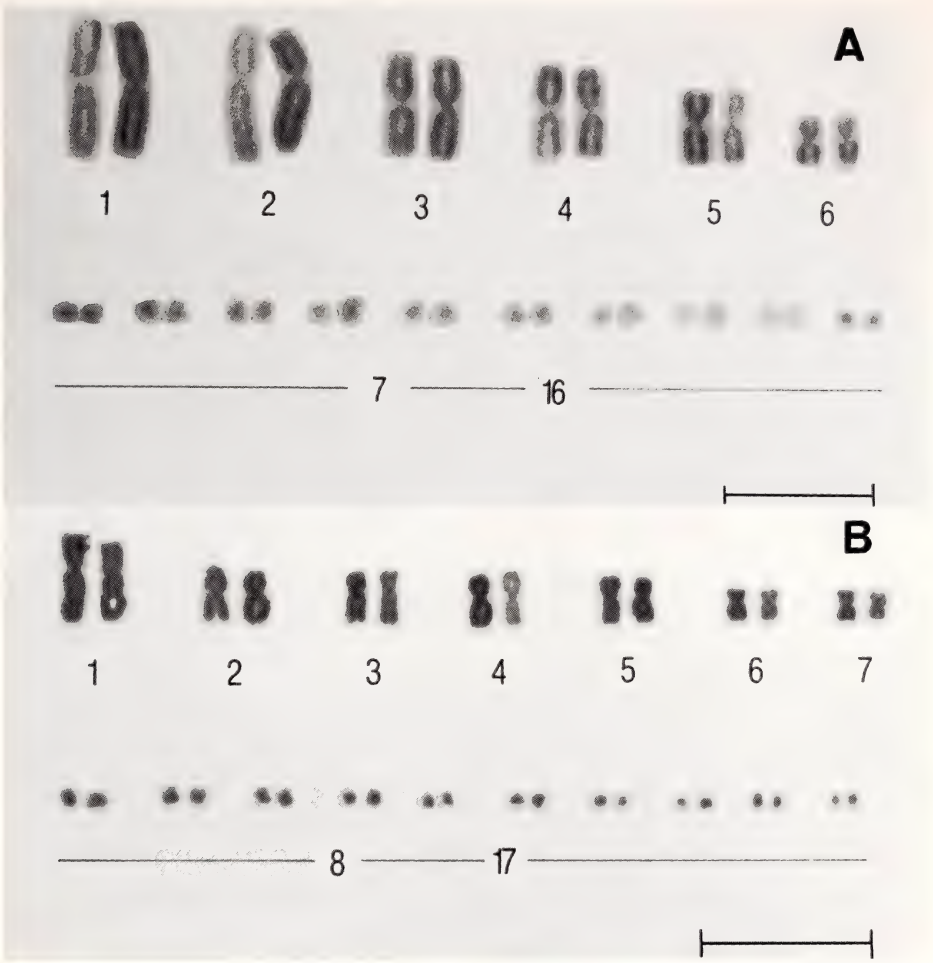

FIG. 1. Male katyotypes of (A) *Acanthosaura armata*, and (B) *Bronchocela cristatella*. Bar equals 5 μm.

The karyotypes of *Calotes emma* and *C. versicolor* were also similar to that of *A. armata* in the number (six pairs), shape (metacentric), and size arrangement (prominent gap only between pairs 5 and 6) of macrochromosomes (Fig. 2, Appendix). However, they differed from the *A. armata* karyotype by having an additional pair of microchromosomes, which made the diploid and fundamental numbers 34 and 46, respectively.

In all karyotypes examined, no sex chromosome heteromorphism, or intraspecific chromosomal variations were evident, although female karyotypes were not available for *A. armata, B. cristatella*, and *C. emma*.

DISCUSSION

This is the first chromosomal description for the genus *Acanthosaura*. The karyotype of *A. armata* differs from most other known karyotypes of the group V species (Moody, 1980; Honda et al., 2000) in having only 20 microchromosomes, because most other members of this tropical Asian clade have another pair of microchromosomes (e.g., Moody, 1980; Witten, 1983; Solleder and Schmid, 1988; Ota and Hikida, 1989). Within this group, the 20 microchromosome state is shared only with *Bronchocela cristatella* (see Solleder and Schmid [1988] and below), *Calotes versi-*

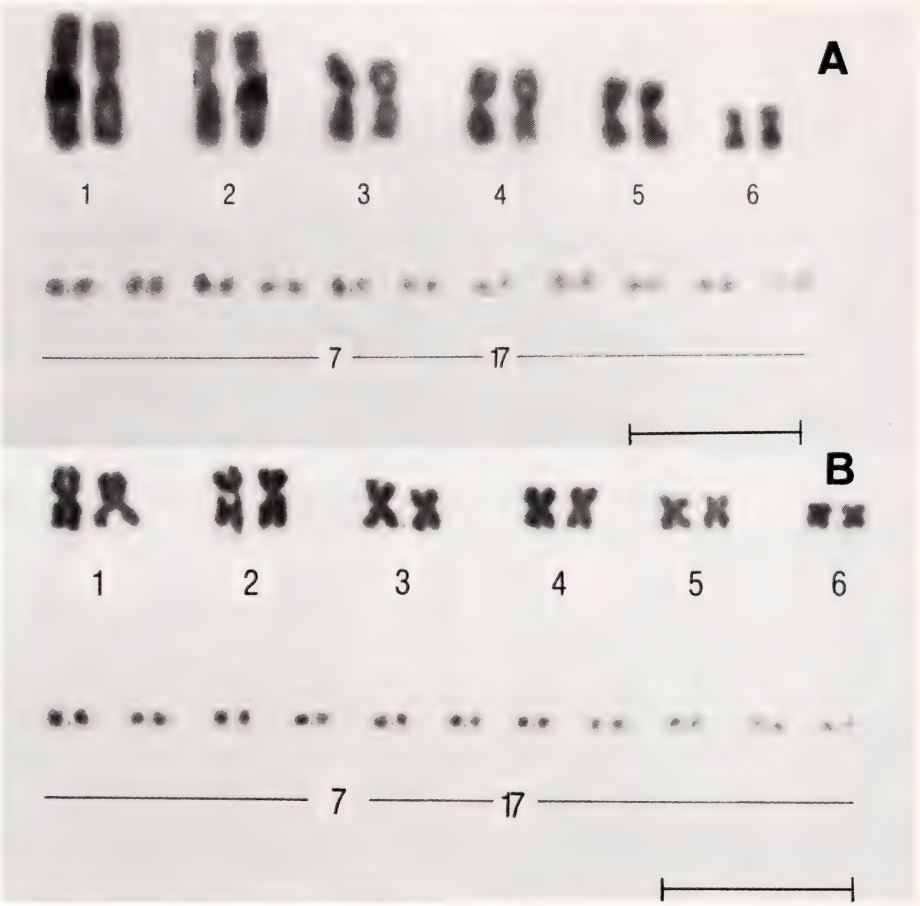

FIG. 2. Male katyotypes of (A) *Calotes emma*, and (B) *C. versicolor*. Bar equals 5 μm.

color in one report (see below), and *Gonocephalus robinsonii* (see Diong et al., 2000). In contrast, this state is common in the clade consisting of groups II–IV of Moody (1980) (see Honda et al. [2000, 2002] and Macey et al. [2000: as the Australian-New Guinean clade]) as pointed out by Witten (1983). Diong et al. (2000), recognizing the common occurrence of 20 microchromosomes in *G. robinsonii* and some Australian-New Guinean species, surmised that *G. robnsonii* might have been derived from endemic Australian radiation, followed by long dispersals like *Physignathus cocincinus* (Honda et al., 2000). This view, however, was negated by a molecular phylogenetic investigation by Honda et al. (2002), which clearly indicated the allocation of *G. robinsonii* in group V. Likewise, recent molecular phylogenetic studies (Honda et al., 2000, 2002; Macey et al. 2000) negate a close affinity of *Acanthosaura* with the Australian-New Guinean agamids, although none of these studies examined *A. armata*. Relatively close allocation of *Acanthosaura* (as represented by *A. crucigera*) with *G. robinsonii* on the molecular phylogenetic tree of Honda et al. (2002) suggests that the deletion of a pair of microchromosomes may have occurred in their common ancestral lineage. This assumtion needs substantial verification on the basis of additional chromosomal data for relevant taxa, particularly *A. crucigera* and other *Acanthosaura* and *Phoxophrys* species (Honda et al., 2002).

The karyotypes of *B. cristatella*, *C. emma*, and *C. versicolor* were already reported in

TABLE 2. Karyotypes of the four agamid species examined in this study. M=macrochromosomes; m=microchromosomes. Sources are as follows: 1, this study; 2, Solleder and Schmid (1988); 3, Moody (1980); 4, De Smet (1981); 5, Singh and Bhatnagar (1987); 6, papers cited in Das and Ota (1998) exclusive of 4 and 5.

Species	2n	Arm nos. in macrochromosomes	Chromosomal formula	Source
Acanthosaura armata	32	24	12M + 20m	1
Bronchocela cristatella	34	28	14M + 20m	1, 2
	48	28	28M + 20m	3
Calotes emma	34	24	12M + 22m	1, 2
Calotes versicolor	34	24	12M + 22m	1, 6
	32	24	12M + 20m	4
	34–62	24	12M + (22–50)m	5

some previous studies (Table 2). However, absence of locality data for materials used in most of those studies makes our data deserving of publication, because our data may contribute to the detection of cryptic taxonomic diversity in those species (Ota et al., 2001). For example, Moody (1980), on the basis of unpublished information from W. P. Hall, listed the karyotype of *B. cristatella* as consisting of 28 acrocentric macrochromosomes and 20 microcromosomes, an arrangement dramatically different from the "conspecific" karyotype subsequently reported by Solleder and Schmid (1988), and in the present study (Table 2). It is thus likely that *B. cristatella* in the current definition actually contains more than one species.

In *C. versicolor*, the microchromosome number seems to vary, because, although most authors reported the number to be 22, De Smet (1981) described one male of unknown locality as having 20 microchromosomes only. Furthermore, Singh and Bhatnagar (1987) reported a remarkable variation in the microchromosome number in some Indian materials (Table 2). Although one or both of these records may simply have resulted from the miscounting of those tiny elements, it is not surprizing if *C. versicolor* in the current definition is actually a composite of more than one cryptic species with different microchromosome numbers, considering the extensive morphological variation in this broadly distributed species (Auffenberg and Rehman, 1993).

In both cases, absence of reliable locality information in most crucial works (Hall in Moody [1980], and Solleder and Schmid [1988] for the *B. cristatella* karyotype; and De Smet [1981], and a few other works [Table 2] for the *C. versicolor* karyotype) imposes serious difficulties in utilizing their chromosomal data for unequivocal solutions of taxonomic problems implied therein. Accumulation of chromosomal data with reliable locality information and voucher specimens is definitely needed for the appropriate estimation of taxonomic diversity in these and other agamid species from Southeast Asia.

ACKNOWLEDGMENTS

We thank the Institute of Biological Sciences, University of Malaya, Kuala Lumpur, for provision of facilities for experiments. This study was partially supported by an Academic Research Grant from the Nanyang Technological University of Singapore (No. RP21/97, to CHD).

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APPENDIX

Quantitative morphological data for macrochromosomes of the four agamid species examined in this study ($\bar{x}\pm SD$). Abbreviations are: AA, *Acanthosaura armata*; BC, *Bronchocela cristatella*; CE, *Calotes emma*; CV, *Calotes versicolor*; RR, relative length (%); AR, arm ratio (or centromeric ratio).

		Macrochromosome pairs						
		1	2	3	4	5	6	7
AA	RR	23.08	20.22	17.92	15.79	13.37	9.65	
		±1.14	±1.23	±1.14	±0.72	±1.50	±1.29	
	AR	1.18	1.26	1.19	1.18	1.12	1.15	
		±0.15	±0.22	±0.14	±0.08	±0.11	±0.17	
BC	RR	22.38	16.52	15.40	14.33	12.55	10.07	8.60
		±1.52	±1.48	±0.80	±0.85	±0.77	±0.99	±1.15
	AR	1.51	1.37	1.29	1.28	1.12	1.29	1.20
		±0.26	±0.38	±0.31	±0.17	±0.16	±0.28	±0.16
CE	RR	22.31	21.48	16.82	16.03	13.75	9.61	
		±1.07	±0.38	±0.51	±0.90	±1.15	±0.04	
	AR	1.08	1.33	1.09	1.12	1.20	1.12	
		±0.08	±0.22	±0.05	±0.08	±0.10	±0.07	
CV	RR	23.31	20.86	16.86	16.12	13.36	9.49	
		±0.50	±1.74	±0.48	±1.02	±0.67	±1.13	
	AR	1.31	1.38	1.13	1.17	1.17	1.12	
		±0.32	±0.29	±0.21	±0.11	±0.21	±0.10	

Accepted: 31 May 2002

Current Herpetology 21(1): 43–50, June 2002

Early Growth of *Elaphe quadrivirgata* from an Insular Gigantic Population

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Abstract: ***Elaphe quadrivirgata*** **on Tadanae-jima Island shows a clear insular gigantism. Based on data from captive animals, we compared growth rates over the first two years after hatching between this population and a conspecific population from the Japan mainland. The purpose of this experiment was to test the hypothesis that early growth rates in snakes in the insular gigantism population are higher than those in conspecific non-gigantic populations under the same feeding schedule. Growth rates in snout-vent length and body mass of Tadanae-jima snakes were not higher than those of main island snakes, and thus, the hypothesis was rejected. This result suggests that the gigantism in *E. quadrivirgata* on Tadanae-jima Island is not caused by a genetically based modification for rapid growth before maturation.**

Key words: *Elaphe quadrivirgata*; Growth; Izu Islands; Insular gigantism; Snake

INTRODUCTION

Body size is a fundamental character that affects almost all life history traits of animals (Schmidt-Nielsen, 1984). Intraspecific geographic variations in body size would, therefore, offer important opportunities to study microevolution of organisms. To understand the process of microevolution, it is essential to elucidate the proximate factors that cause the phenotypic variation in body size.

Insular gigantism is a notable example of geographic body size variations and has been reported in many animal taxa including snakes (Case, 1978; Schwaner, 1985; Hasegawa and Moriguchi, 1989; King, 1989; Kohno and Ota, 1991; Mori, 1994; Mori et al., 1999). Practically, gigantism is determined by comparing standard sizes of animals among populations, i.e., average or maximum sizes of mature individuals. In snakes, which show asymptotic growth after maturity, gigantism can be caused by several mechanisms and proximate factors that are not mutually exclusive: differences in age structure, growth rates, size at maturity, or asymptotic size (Stamps, 1993). Each of these differences may stem from either genetically based local adaptations or phenotypically plastic variations largely due to local environmental conditions such as high abun-

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dance of food resources.

Elaphe quadrivirgata is a common colubrid snake widely distributed in Japan including small islands adjacent to the main islands. Insular body size variation in this snake has been documented for populations of the Izu Islands, located off the south of the central part of Honshu Island, the largest island of Japan (Hasegawa and Moriguchi, 1989). Among these, snakes on Tadanae-jima Island, an uninhabited islet with an area of 0.01 km^2, show a remarkable gigantism in adult body size, being more than three times larger in body mass than snakes of other adjacent islands (Hasegawa and Moriguchi, 1989) and of Honshu Island (Fukada, 1992; Kadowaki, 1996; Mori, unpublished data).

As a part of a long term ecological and behavioral study of *E. quadrivirgata* of the Izu Islands, we investigated possible mechanisms of the gigantism of *E. quadrivirgata* on Tadanae-jima Island. Higher growth rate is one of the possible factors that causes the gigantism and could result from differences in food supply (even only during early life, see Madsen and Shine, 2000), food type, and/or physiological efficiencies. Here, we tested the hypothesis that the juvenile *E. quadrivirgata* of Tadanae-jima island show higher growth rates than those of Honshu Island. The underlying hypothesis for differential growth rates is a genetically based modification in physiological traits, such as higher energy assimilation and lower energy expenditure (Angilletta, 2001a, b) of the former. We reared hatchlings from Tadanae-jima and Honshu under the same feeding schedule for approximately two years and compared their growth patterns.

Materials and Methods

The subjects were neonate *E. quadrivirgata* hatched in the laboratory from eggs laid by wild-caught gravid snakes. A male and a female hatchling were randomly selected from each of eight clutches oviposited by females (snout-vent length: SVL, range, 1007–1292 mm, $\bar{x}$=1147 mm, body mass: BM, range, 361–972 g, $\bar{x}$=631 g) collected from Tadanae-jima Island (34°13′N, 139°12′E) in June 1994. Six hatchlings (two males and four females) from a single clutch of a female (SVL=680 mm, BM=147 g) collected from Tokai-mura, Ibaraki Prefecture (36°30'N, 140°30'E), Honshu, were used for comparisons. Although quantitative body size data of *E. quadrivirgata* in this population is not available, we assumed, based on the body size data of *E. quadrivirgata* in various areas of Honshu and the Izu Islands (Hasegawa and Moriguchi, 1989; Fukada, 1992; Kadowaki, 1996; Mori, unpublished data), that average body size of the snakes in Tokai-mura is well within the size range of *E. quadrivirgata* in Honshu and considerably smaller than that of the Tadanae-jima population.

Newly hatched snakes were weighed (BM), measured (SVL), and then housed individually in white polypropylene (190×140×70 mm) cages, each containing a water dish and paper floor covering. As the snakes grew larger (ca. one year after hatching), they were moved to larger plastic cages (320×180×260 mm). The temperature varied between 25 and 30 C except winter, when the snakes were induced to hibernate. Illumination was provided by sunlight.

During the first month after hatching in 1994, small frogs (*Hyla japonica* and *Rana limnocharis*) or lizards (*Eumeces okadae*) were offered to the snakes. Thereafter, because of unavailability of small live food, the snakes were raised by force feeding (Frye, 1991) until 11 May 1995. In this period, beef liver mixed with a multivitamin supplement and calcium powder and lubricated with raw egg was provided to each individual. From 16 May 1995, live suckling mice (*Mus musculus*) were provided. If the snakes did not spontaneously eat the mice a day after their introduction, the mice were fed to the snakes by force feeding. Food items were provided basically twice a week except for the hibernation period (from mid November to mid April). Although the weight of food varied during the study period (0.4–6.4 g),

approximately the same amount of food was offered to each of the snakes on each feeding day.

In 1994, SVL and BM were measured immediately before hibernation. In 1995 and 1996, these measurements were taken approximately every month except during the hibernation period. This study was focused on the growth pattern before maturation, which can occur as early as the age two years (see Fukada, 1992), and therefore the study was terminated before the beginning of the third hibernation. Growth rates in SVL and BM were calculated for each measurement day

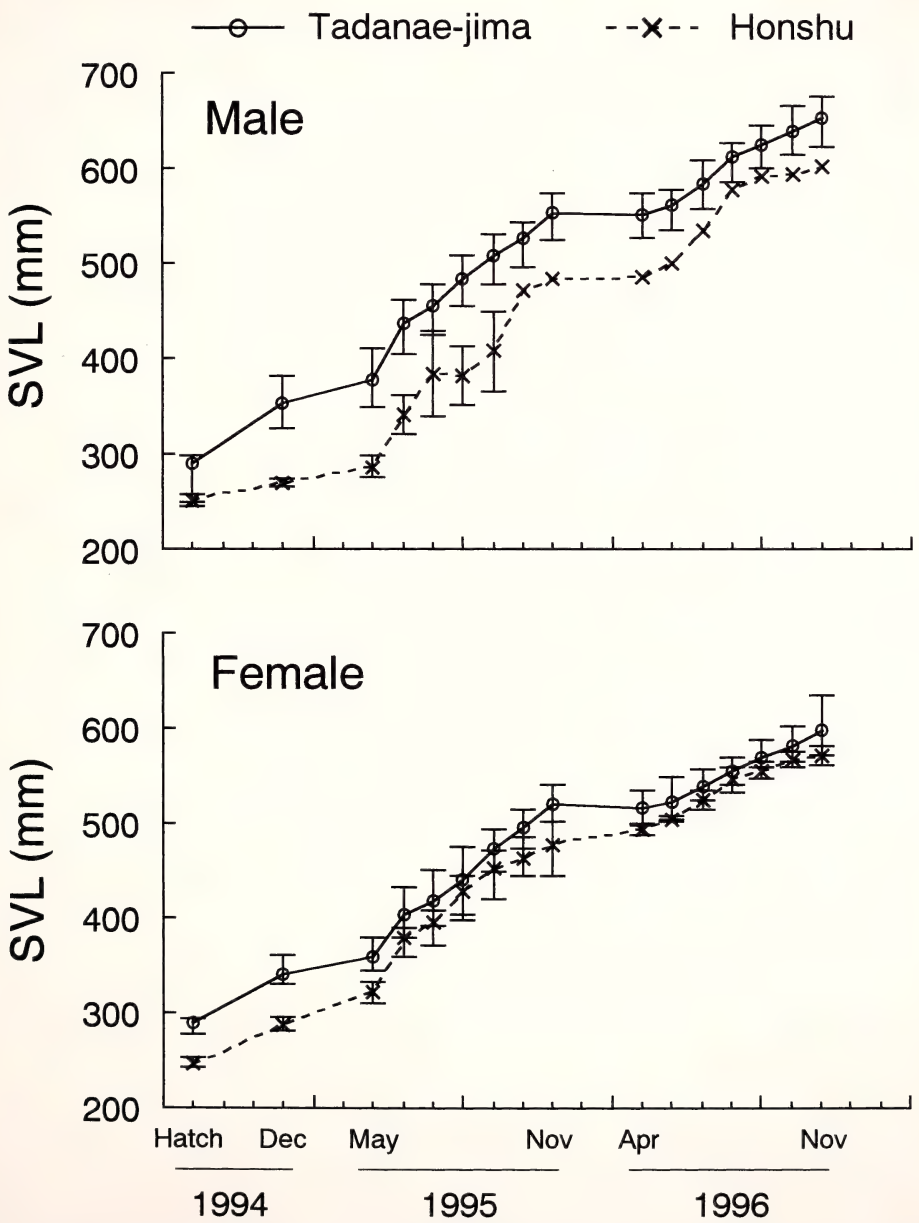

FIG. 1. Growth trajectories of captive *Elaphe quadrivirgata* from populations on a Japan main island (Honshu) and an islet of the Izu Islands (Tadanae-jima). Each point shows the mean snout-vent length (SVL). Vertical bars show range.

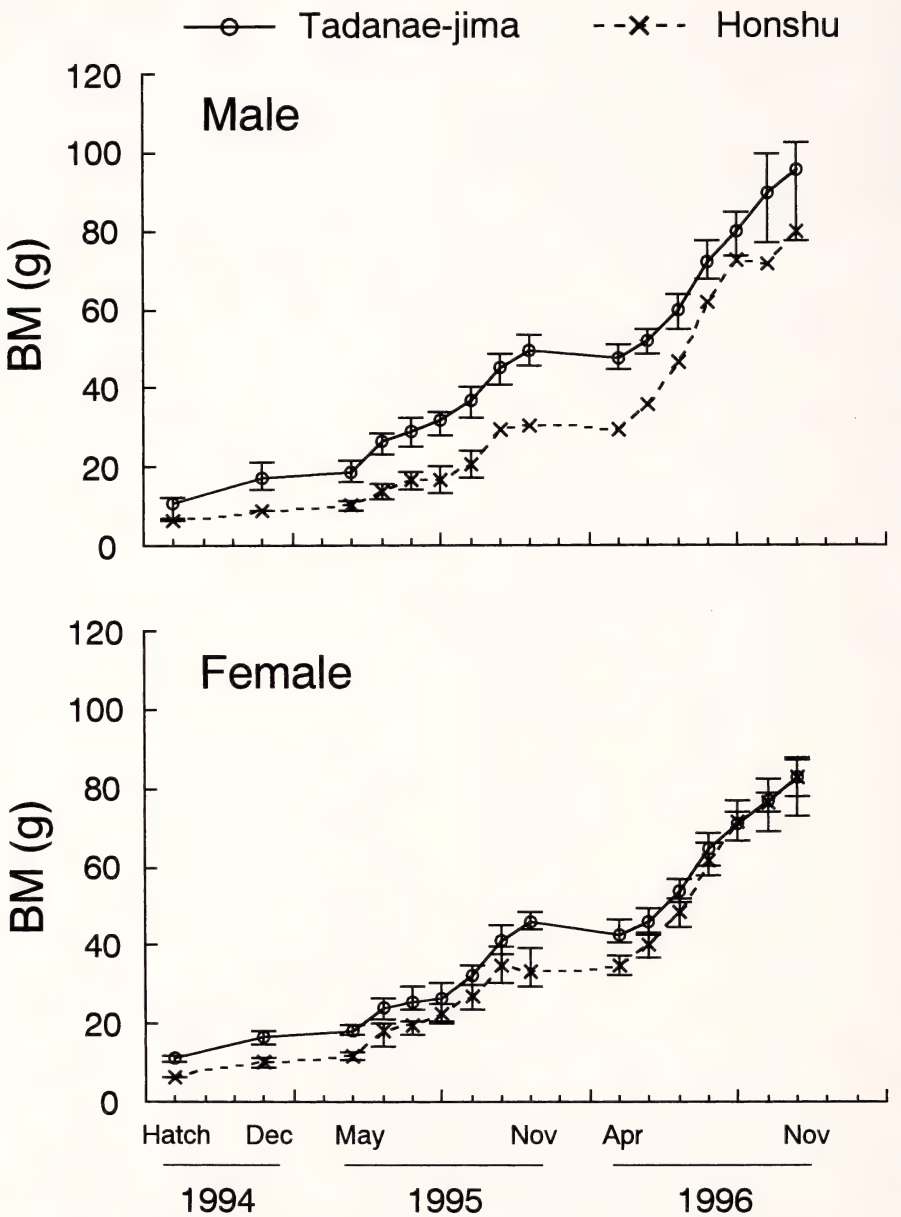

FIG. 2. Growth trajectories of captive *Elaphe quadrivirgata* from populations on a Japan main island (Honshu) and an islet of the Izu Islands (Tadanae-jima). Each point shows the mean body mass (BM). Vertical bars show range.

as: increment in SVL (BM)/SVL (BM) at the last measurement/elapsed days.

RESULTS

At hatching, no significant sexual differences in SVL and BM were detected either in Tadanae-jima or Honshu snakes (all $P>0.20$), and so the sexes were pooled for the following analysis. Hatchlings of Tadanae-jima were significantly larger in SVL and BM than those of Honshu (SVL: Tadanae-

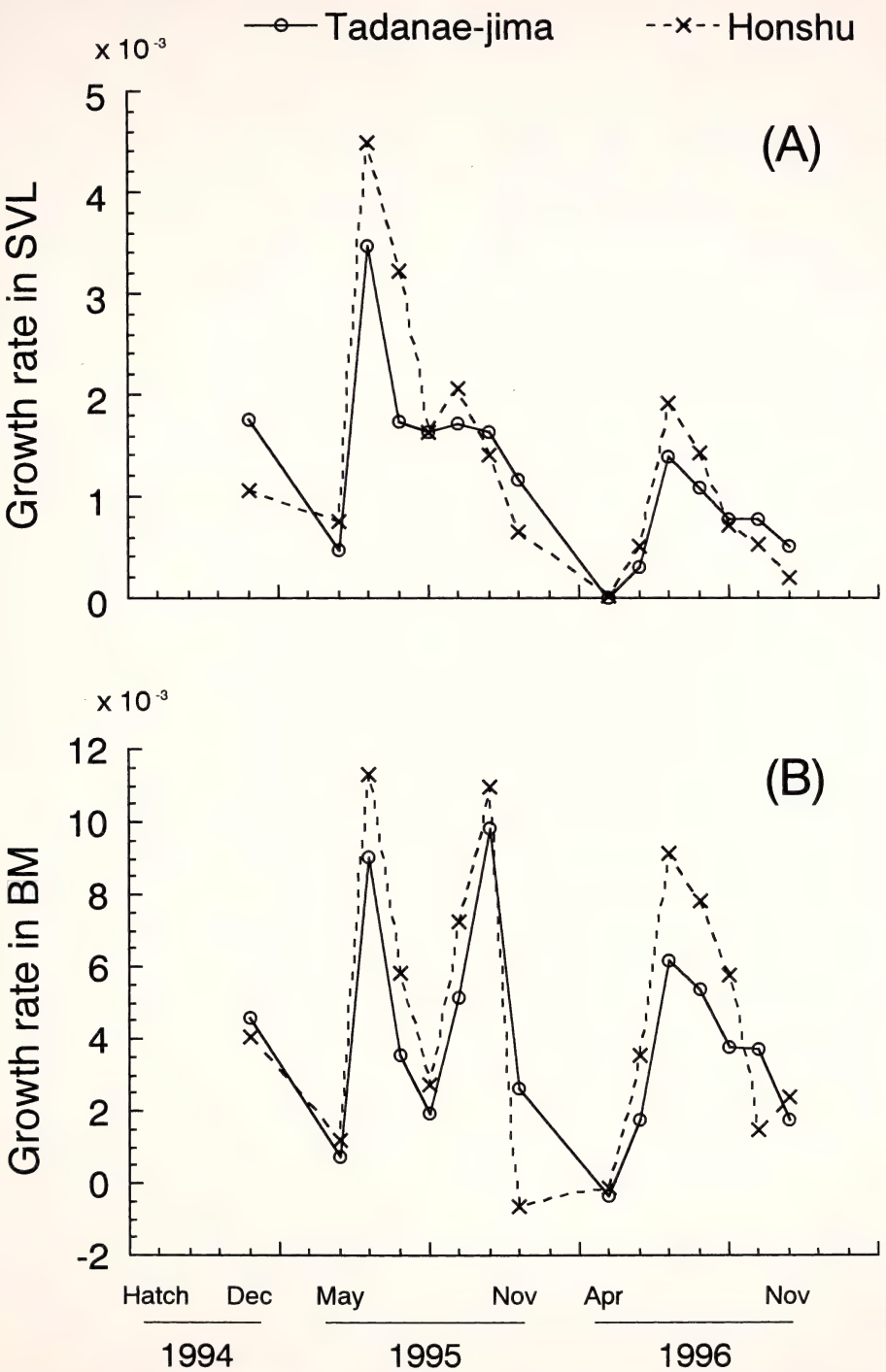

FIG. 3. Growth rates in snout-vent length (SVL: A) and body mass (BM: B) for captive *Elaphe quadrivirgata* from populations on a Japan main island (Honshu) and an islet of the Izu Islands (Tadanae-jima). Each point shows mean growth rate. Growth rates were calculated as: increment in SVL (BM)/SVL (BM) at the last measurement/elapsed days.

jima, $\bar{x}$=290 mm, Honshu, $\bar{x}$=249 mm, Mann-Whitney U-test, U=94, P<0.001; BM: Tadanae-jima, $\bar{x}$=11.2 g, Honshu, $\bar{x}$=6.5 g, Mann-Whitney U-test, U=96, P<0.0005).

Growth patterns were very similar between the two populations both in SVL and BM (Figs. 1 and 2). No higher growth rates were evident in the Tadanae-jima snakes (Fig. 3). In contrast, growth rates seemed to be higher in Honshu snakes. Accordingly, the between-population differences in SVL and BM, apparent at the hatching stage, gradually decreased toward the end of the study (Figs. 1 and 2). Both SVL and BM at the final measurement (November 1996) were not significantly different between the two populations (SVL: Tadanae-jima, $\bar{x}$=627 mm, Honshu, $\bar{x}$=582 mm, Mann-Whitney U-test, U=34, P=0.051; BM: Tadanae-jima, $\bar{x}$=89.3 g, Honshu, $\bar{x}$=81.8 g, Mann-Whitney U-test, U=28, P>0.25: sexes were pooled for these statistical tests because there were no significant sexual differences at this age). Two and three snakes of Tadanae-jima and Honshu, respectively, died during the course of the study.

A close inspection of Fig. 3 revealed a subtle difference in growth pattern between Tadanae-jima and Honshu snakes. In both SVL and BM, average growth rates of Tadanae-jima snakes were greater than those of Honshu snakes only before hibernation (i.e., October to November). This trend was observed in all three years.

Discussion

Differences in body sizes among populations of *E. quadrivirgata* could arise from several factors. They could, for example, result from genetic differences among populations due to selective pressures, genetic drift, or both. Alternatively, phenotypic differences could directly result from more proximate differences in environmental conditions such as food availability, duration of activity season, and temperature. Even if snakes of different populations have the same growth trajectories, differences in average body size could arise as a mere result of difference in age structure: i.e., average body sizes of snakes from populations consisting of older individuals could be larger than those of younger ones.

Our experiment was aimed to test the hypothesis that gigantism of *E. quadrivirgata* on Tadanae-jima island is caused by genetically based high growth rates before maturation. The present result does not support this hypothesis, as the growth rates of the two samples compared were basically similar. Average growth rates were even higher in the Honshu snakes than in the Tadanae-jima snakes. Non-facilitated growth rates of Tadanae-jima snakes were also confirmed when their growth rates were compared with those of *E. quadrivirgata* under natural conditions in Kyoto Prefecture, Honshu Island (Fukada, 1992). Therefore, it is likely that the gigantism of *E. quadrivirgata* on Tadanae-jima is attributable to greater and/or continuous growth of adult snakes with abundant food resources, such as eggs and nestlings of sea birds (Hasegawa and Moriguchi, 1989). Nonetheless, differential body size among populations of the Izu Islands may not be sufficiently explained on the grounds of pure phenotypic plasticity, and the possibility that other growth parameters, such as maturity and asymptotic sizes, are genetically determined cannot be excluded at present (see Wikelski et al., 1997).

Several experimental studies have been conducted to clarify which of the above mentioned factors are responsible for geographic size differences in snakes. Barnett and Schwaner (1985) reported that neonates from an insular gigantic population of *Notechis ater* reared under laboratory conditions with ad libitum feeding grew faster than those of a mainland conspecific population under natural conditions. In addition, Schwaner (1985) briefly reported that *N. ater* from another gigantic island population grew faster than that from a dwarfed island population when reared with the same amount of food,

concluding that geographic size variation is genetically controlled. Similarly, Bronikowski (2000) showed, based on the results of a common-garden growth experiment, that field variation in growth in *Thamnophis elegans* has a genetic basis. Forsman (1991) attributed the difference in body size between the island populations of *Vipera berus* to difference in growth rate rather than difference in age structure, based on the growth data of wild snakes. On the other hand, Madsen and Shine (1993) compared growth rates of mainland *Natrix natrix* with those of an island dwarf population under laboratory conditions over six years and concluded that the differences in adult body size between these populations result from direct influence of prey availability without any genetic modification.

These results, coupled with the present one, indicate the presence of diverse mechanisms responsible for geographic variations of body size in snakes. Such diversity may be partially attributable to the differences in local environmental conditions and historical backgrounds. Studies on geographic variations of body size in snakes would offer splendid opportunities to unravel the adaptive microevolution and evolutionary significance of phenotypic plasticity.

Two observations should be noted here. First, the subtle but consistent difference in growth patterns between Tadanae-jima and Honshu snakes, that is, higher growth rates in the former only before hibernation, may imply that some genetic-based differences in growth pattern are present between them. Light cycle, time of the year, or temperature (although room temperature was kept between 25 and 30 C during the feeding period, average temperature varied seasonally within this range) may have interacted with genetically determined physiological traits of the source populations to influence growth pattern (Bronikowski, 2000).

Second, we emphasize that explicit discrimination between gigantism of adult snakes and large size of hatchlings should be made when we examine the causal mechanisms of geographic size variations in snakes. Although it is likely that neonate size is affected by size and nutritional conditions of maternal snakes (e. g., Ford and Seigel, 1989), larger hatchling size of Tadanae-jima population than populations of adjacent islands and Honshu seems to be, at least partially, genetically determined, because allometric relationships between maternal snake sizes and their offspring sizes are different between Tadanae-jima and the other populations. (Hasegawa, unpublished data). Because of gape limitation in snakes, larger hatchlings having larger gape size would have the advantage of being able to exploit a wider size range of prey. This may be especially true on Tadanae-jima Island, where potential prey animals available to small snakes are limited (Hasegawa and Moriguchi, 1989). On the other hand, larger body size of adults on Tadanae-jima might reflect a phenotypic response to the high food availability, as well as an adaptation for delayed maturation that facilitates growth and enables them to exploit food resources available only for large individuals (eggs and nestlings of sea birds). This scenario considers larger hatchling size as a local adaptation, and gigantism in adult snakes as representing a complexity of phenotypic plasticity and local adaptation. In any event, hatchling size and adult size (standard size) should be considered separately when mechanisms of geographic body size variations are studied, especially in snakes, where ingestible prey are quite different between hatchlings and adults because of gape limitation.

ACKNOWLEDGMENTS

We wish to thank many colleagues in Kyoto University for their assistance in keeping animals. M. Honda provided a snake collected in his home town. This study was partially supported by grants from the Fujiwara Natural History Foundation, the Pro-Natulra Foundation, and the research project of the

National Institute of Environment on conservation methods of subtropical island ecosystems awarded to M. Hasegawa.

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Accepted: 13 June 2002

Current Herpetology 21(1): 51–53, June 2002

On the Authorship of *Babina* (Ampbibia: Ranidae)

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Abstract: The genus-group name *Babina*, originally proposed as a full genus for *Rana holsti* (type species) and *R. subaspera*, is usually attributed to "Van Denburgh, 1912". However, it is obvious from the chronological order of publication of relevant papers that the authorship of *Babina* should be "Thompson, 1912", not "Van Denburgh, 1912".

Key words: *Babina*; Ranidae, Anura; Nomenclature; Authorship; Priority

The genus-group name *Babina* was first published in 1912 by two different authors, Thompson (1912a) and Van Denburgh (1912a). In both of these papers, the name was given to a new full genus described to accommodate two endemic frogs of the central Ryukyus, *Rana holsti* Boulenger, 1892, and *R. subaspera* Barbour, 1908, with the former being the type species. Also, both Thompson (1912a) and Van Denburgh (1912a) highlighted a sharp, spine-like metacarpal on the inner side of the first finger in these two species as the prominent character distinguishing *Babina* from other ranid genera.

Van Denburgh published a more detailed description of the genus, without referring to Thompson's (1912a) description, in his famous work on the East Asian herpetofauna published later in the same year (Van Denburgh, 1912b). Probably because both of the preceding descriptions were privately published by the respective authors and thus suffered limited availability, Van Denburgh (1912b) seems to have been regarded as the only source of information on the original description of *Babina* by most subsequent authors. Some of them (e.g., Okada [1930], p. 154) even erroneously referred to Van Denburgh (1912b) as the original description of the genus, although it was unequivocally stated on Van Denburgh's (1912b) second page that a number of his new taxa (including *Babina*) were originally described in Van Denburgh (1912a).

Of the subsequent authors, some considered *Babina* as invalid (Inger, 1947; Dubois, 1981), others continued to use the name as a valid full genus (Okada, 1930, 1966), whereas most recent authors regard *Babina* as a subgenus of *Rana* (Nakamura and Uéno, 1963; Kuramoto, 1972; Matsui and Utsunomiya, 1983; Frost, 1985; Maeda and Matsui, 1989; Dubois, 1992; Duellman, 1993). In any event, authorship of this genus-group name has invariably been given as "Van Denburgh, 1912" (e.g., Okada, 1930, 1966; Inger, 1947; Nakamura and Uéno, 1963; Dubois, 1992; Duellman, 1993).

In 1912, Thompson and Van Denburgh separately described a number of East Asian amphibians and reptiles on the basis of the same series of specimens (and sometimes even on the basis of exactly identical holotype specimens) in rivalry with each other (Zhao and Adler, 1993: p. 32), and this resulted in a "most regrettable tangle of names" (Barbour, 1917; Nakamura and Uéno, 1963; Zhao and Adler, 1993). Nakamura and Uéno (1963) referred to this confusing situation with an example of the authorship of *Hyla hallowellii*, a species described by both Thompson (1912b) and Van Denburgh (1912a). While severely criticizing Thompson's actions, Nakamura and Uéno (1963) argued that the name, usually given as "*Hyla hallowellii* Van Denburgh, 1912" to

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that date (e.g., Okada, 1930; Inger, 1947), should be attributed to "Thompson, 1912", recognizing that Thompson (1912b) had preceded Van Denburgh (1912a) by approximately one month. Nakamura and Uéno (1963), nevertheless, continued to regard "Van Denburgh, 1912" as the author of *Babina*, although Thompson (1912a: Herpetological notices 1) should have preceded Thompson (1912b: Herpetological notices 2) in publication date.

Based on the date printed in each of the relevant papers, Zhao and Adler (1993) confirmed the chronological order of their publications as Thompson (1912a: on 15 June), Thompson (1912b: 28 June), Van Denburgh (1912a: on 29 July), and Van Denburgh (1912b: on 16 December). It is thus obvious from the principle of priority of the International Code of Zoological Nomenclature (2000) that Thompson (1912a) should be regarded as the author of the original description of *Babina*. Thus, the authorship of this genus-group name should be "Thompson, 1912", not "Van Denburgh, 1912".

Acknowledgments

We thank K. Adler and R. I. Crombie for the provision of pertinent literature.

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Accepted: 12 May 2002

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(Reptilia: Bataguridae)

The author's name should be centered, with all letters capitalized. In the case of more than one author, indicate the one to whom communications regarding the paper after publication should be directed, with his/her telephone and fax numbers, and e-mail address. Affiliation(s) and address(es) of the author(s) should be centered, and in italics (indicated by underlining) with only the initial letter of each major word capitalized: e.g.,

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Abstract page

The abstract page should contain an abstract consisting of less than 250 words, followed by one blank line and by key words in order. The abstract should state the major points of the paper as clearly and concisely as possible without the need for reference to the text and without citation of references. The word "Abstract" should not be indented, and should be followed by a colon: e.g.,

> Abstract: Monophyly of the batagurid subfamily Geoemydinae was evaluated .....

The term, "Key words", should not be indented, and should be followed by a colon and then by about five key words, separated from each other by semicolons, that identify the major aspects of the manuscript: e.g.,

> Key words: Geoemydinae; Bataguridae; Phylogeny; Geoemyda group; Mauremys group

The main text

Texts of most manuscripts are efficiently arranged in order of introduction, materials and methods, results, discussion, and acknowledgments; however, some manuscripts, particularly of reviews and short notes, profit by other arrangements of topics, so the author(s) should use good judgment in this matter. **Italics, indicated by underlining, should be used only for scientific names of genera, species and/or subspecies, and for appropriate headings** (see below). Commonly used words of non-English origins should not be italicized (e.g., et al., not et al.).

Up to three sets of headings are allowed. The major heading, all capitalized, should be centered. The subheading should be centered and underlined (indication of italics in final

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References

The reference section following the main text should begin with the major heading, LITERATURE CITED, and **list all and only the publications cited in the manuscript** in alphabetical order according to the senior authors' surnames. When there are several papers by the same senior author with various co-authors, they should be listed in alphabetical order by second and subsequent authors, regardless of the number of authors. Following are examples for the format and order of listing of references.

AOKI, R. 2001. Wani To Ryu [Crocodiles and Dragons]. Heybonsha, Tokyo. 239 p. (in Japanese)

FUKADA, H. 2002. A brief history of the Herpetological Society of Japan. Bull. Herpetol. Soc. Japan 2002(1): 13-17. (in Japanese)

HIRATE, K. 2000. Species Composition, Sex Ratio, Size Distribution, and Seasonal Fluctuation of the Sea Turtle Assemblage in the Eastern Off-shore of the Central Part of Okinawajima. Unpublished master's thesis. University of the Ryukyus, Nishihara. 68 p. (in Japanese)

HONDA, M, Y. YASUKAWA, AND H. OTA. In press. Phylogeny of the Eurasian freshwater turtles of the genus Mauremys Gray, 1869 (Testudines). J. Zool. Syst. Evol. Res.

KAMEZAKI, N. 1989. The nesting sites of sea turtles in the Ryukyu Archipelago and Taiwan. p. 342-348. In: M. Matsui, T. Hikida, and R. C. Goris (eds.), Current Herpetology in East Asia. Herpetological Society of Japan, Kyoto.

LEVITON, A. E. AND R. H. GIBBS, Jr. 1988. Standards in herpetology and ichthyology. Standard symbolic codes for institution resource collections in herpetology and ichthyology. Supplement no. 1: additions and corrections. Copeia 1988(1): 280-282.

LEVITON, A. E., R. H. GIBBS, Jr., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985(3): 802-832.

MATSUI, M. 1987. Isozyme variation in salamanders of the nebulosus-lichenatus complex of the genus Hynobius from eastern Honshu, Japan, with a description of a new species. Jpn. J. Herpetol. 12(2): 50-64.

MATSUI, M., H. IWASAWA, H. TAKAHASHI, T. HAYASHI, AND M. KUMAKURA. 1992a. Invalid specific status of Hynobius sadoensis Sato: electrophoretic evidence (Amphibia: Caudata). J. Herpetol. 26(4): 308-315.

MATSUI, M. AND K. MIYAZAKI. 1984. Hynobius takedai (Amphibia, Urodela), a new species of salamander from Japan. Zool. Sci. 1(6): 665-671.

MATSUI, M., T. SATO, S. TANABE, AND T. HAYASHI. 1992b. Electrophoretic analyses of systematic relationships and status of two hynobiid salamanders from Hokkaido (Amphibia: Caudata). Herpetologica 48(4): 408-416.

MOODY, S. M. 1980. Phylogenetic and Historical Biogeographical Relationships of the Genera in the Family Agamidae (Reptilia: Lacertilia). Unpublished doctoral dissertation. University of Michigan, Ann Arbor. 373 p.

TAKENAKA, T. 2000. Extinction of the naturalized freshwater turtle in Chichijima-Island of Ogasawara (Bonin) Islands, South Japan. Bull. Herpetol. Soc. Japan 2000(1): 4-7. (in Japanese with English abstract)

ZHAO, E. AND K. ADLER. 1993. Herpetology of China. Contribution to Herpetology, 10. Society for the Study of Amphibians and Reptiles, Oxford, Ohio. 522 p.

In the text, references to papers by one or two authors should give their surnames; papers with more than two authors are referenced by the first author's surname followed by "et al.". Strings of references should be placed in chronological order. When there are two or more references published in a same year, they should be arranged in alphabetical order. Two or more references by the same senior author (for papers by one or more than two authors) or by the same senior and junior authors (for papers by two authors) with the same year of publication should be designated by lowercase letters: e.g., (Matsui et al., 1992a, b). See above for example of listing of such references in LITERATURE CITED.

For references that are in the course of publication (i.e., already accepted for publication but not published yet), cite "In press" in the place of publication year and leave the place of page numbers blank. **References of unpublished master's theses and unpublished doctoral dissertations are not encouraged**, but are allowed when their citations are definitely needed (see above for example of listing of such references in LITERATURE CITED). **The other manuscripts that are neither "In press" nor published should not be cited** either in the text or in LITERATURE CITED.

Appendices

Detailed information not essential to the text but important to subsequent evaluation (such as that regarding specimens examined) may be placed under the major heading, APPENDIX, and an appropriate sub-subheading. When institutional abbreviations are used in APPENDIX, and/or in the main text, it is recommended, as far as possible, to follow Leviton et al. (1985) or Leviton and Gibbs (1988) (see example of references above for detailed information on these publications) with an explicit statement in APPENDIX (or otherwise, in MATERIALS AND METHODS of the main text): e.g.,

APPENDIX

Specimens examined

Catalogue numbers of specimens deposited in the zoological collection of Kyoto University Museum are preceded by KUZ. The other acronyms are those suggested by Leviton et al. (1985).

Geoemyda japonica: Okinawajima, Okinawa Pref., Japan, KUZ R36720, NSMT H02083-02086; Kumejima, Okinawa Pref., Japan, KUZ R36721, OMNH-R3334. G. spengleri: Vietnam, NSMT H9999, ...

Use major headings with consecutive Roman numerals, APPENDIX I, APPENDIX II, APPENDIX III, APPENDIX IV, etc., when two or more appendices are needed.

Tables

Each table should be typed, double-spaced, **on a separate sheet. Its appropriate position in the text should be marked in the right-hand margin** (usually at the place where the table is first mentioned). The legend for a table should follow the table number (e.g., TABLE 1.

Measurements of specimens of .....) and **should be on the same pages as the table**. Within the table, only the initial letter of the first word should be capitalized (e.g., "Adult males"). **Ruled lines should be avoided**. Footnotes (indicated by symbols *, or, *1, *2, *3, etc.) may follow a table when detailed information is needed.

Figures

Figures larger than 28×21 cm cannot be accepted. When several drawings or photographs are to be reproduced as one figure, **they should be mounted on cardboard in the desired arrangement and each of them should be lettered** (A, B, C, etc.). Each figure should be carefully planned to accommodate reduction to a final width of one or two columns in *Current Herpetology*; after reduction, lettering should be≥1.5 mm high and decimals should be visible. Include a scale of distance or dimension where appropriate. Figure legends, each beginning with a fully capitalized abbreviation and a consecutive number (e.g., FIG. 1. Dorsal (A) and lateral (B) views of holotype of .....), should be typed in double space and **grouped together on a separate sheet** with one line of space between them. **Denote in the right-hand margin of the text where each figure should be printed** (usually at the first mention of a figure). In the text, "Figure" should be also abbreviated, but with only the initial letter capitalized (e.g., Fig. 1) except when beginning a sentence. When original figures are sent to the Managing Editor after the acceptance of a manuscript (see above), the back of each figure should be labeled with the author's name, the figure number, and desired size of final reproduction (one column or two columns are the only options).

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Numbers of 10 or larger should be typed as Arabic numerals except at the beginning of a sentence. Numbers one to nine should be spelled out unless they precede units of measurement (e.g., 5 mm), are designators (e.g., experiment 3), or are separated by a figure dash (e.g., 5–7 individuals). The 24-hour clock is used to indicate times of day (e.g., 1900 h); dates should be given by day, month, year in this order (e.g., 5 July 2002). Decimals should not be naked (e.g., 0.5, not .5).

Abbreviations

Weights and measures follow the International System of Units (SI), and such abbreviations should be used throughout the manuscript. Abbreviations used in *Current Herpetology* without being defined at first usage include:

$\bar{x}$ (mean), n (sample size), N (chromosome number, but see below for the use to refer to "north latitude"), no. (number), yr (year[s]), mo (month[s]), wk (week[s]), h (hour[s]), min (minute[s]), s (second[s]), P (probability), df (degrees of freedom), SD (standard deviation), SE (standard error), NS (not significant), l (liter), kg (kilogram), g (gram), m (meter), cm (centimeter), mm (millimeter), µm (micron), C (degrees Celsius, not °C), asl (above sea level; given as, e.g., 100 m asl), °, ', and " (degrees, minutes, and seconds in geography, respectively), N, S, E, and W (north and south latitudes, and east and west longitudes, respectively, but only when preceded by values with appropriate geographical units; e.g., 15°25'N, 121°43'E).

In figures and tables, names of months can be abbreviated as: Jan (January), Feb (February), Mar (March), Apr (April), May (May), Jun (June), Jul (July), Aug (August), Sep (September), Oct (October), Nov (November), Dec (December). In the text, however, they should be fully spelled.

Other abbreviations, such as SVL (snout-vent length), Myr (million years), and MyrBP (million years before present), can also be used, but **define them at first usage**. Do not use symbols, ♂ and ♀, for male and female, respectively.

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DATE OF PUBLICATION
Current Herpetology, Vol. 20, No. 2,
was mailed 28 December 2001.

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Hokkaido Tokai University, Sapporo, Hokkaido, Japan, 5–6 October 2002
(Sen Takenaka, Chair)